THE DRAMA OF LIFE

"SCIENCE OF LIFE" SERIES

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THE DRAMA OF LIFE

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PREFACE

BIOLOGY is the science of living things. It is a rapidly expanding science, which has now grown so large that it is beginning to divide itself into a number of daughter-sciences.

With this increasing subdivision there comes a tendency for the latest results in the various fields to be known only to specialists, although they may be full of interest and meaning for the lay reader. From each of the different branches he can gather something of consequence if the main results are made accessible to him by being shorn of confusing technical complications. From Systematic Zoology and Botany he can obtain a view of all the different kinds of living things, and of the relations which they bear to each other. From Anatomy and Physiology he can derive an understanding of his body. From a study of Embryology and Reproduction, he can understand his development and his relation to the stream of life. Genetics, a subject of comparatively recent growth, is emerging from a controversial period and is now able to present to him the main principles of heredity with considerable certainty. Evolutionary Biology can trace the actual history of the various forms of life, and in so doing it explains much that is perplexing in their structure and working. Ecology, another recently developed field, is concerned with the different living species, not in isolation, but as interrelated parts of a single web of life; already it has produced results of great service to the breeder and cultivator. Medicine, once the study of diseases, is becoming the study of health. Psychology, in its widest sense, treats of the most fascinating problem of all—

it is just beginning to explain the working and evolution of mind, from its dim origins to its strange and often devious workings in the culminating human species. Any one of these sciences can be studied independently of the rest, but they all interact and illuminate each other.

This volume deals with one only of the many branches of biology. It is in all essentials complete in itself, and can be read as a single treatise.

But it also forms part of a more ambitious project—*The Science of Life*—which aims at presenting, for the lay reader, a complete survey of the main results of biological science. This work was originally published as a single volume. In preparing the present edition the text has been divided into nine separate volumes, each complete in itself and each dealing with one particular division of biology. The opportunity has been taken to correct errors in the text and to bring it up to date. Together the nine volumes form an integrated whole. Accordingly, here and there in this volume, the reader will find references to others. These cross references indicate passages in which the topic under review links on to other subjects. In no case are they essential to the understanding of the argument of the separate volume in which they occur. But the reader interested in heredity, for example, will find that the subject is intimately linked with evolution; while one who is studying the past history of life is likely to discover that this would become still more interesting if he were to have some knowledge of physiology and of animal behaviour. Those who desire to pursue such clues must do so in other volumes of the series.

We hope that this method of making volumes on separate subjects available singly, while at the same time providing the possibility of a more general view in the series as a whole, will prove satisfactory both to readers who propose to concentrate on a single field and to those who have the ambition to study the whole subject of biological science.

CONTENTS

CONTENTS

LIST OF ILLUSTRATIONS

THE DRAMA OF LIFE

CHAPTER I

HABITATS

§ 1. Ways and Worlds of Life.
§ 2. Habitats and their Inhabitants.
§ 3. Ways of getting a Living.
§ 4. The Adjustment of Inhabitant to Habitat

§ 1

Ways and Worlds of Life

THE home of Mr. Everyman is a house in the suburbs, between city and country, with a little garden attached. It is the average home of the civilized man. This small portion of the earth's surface is the abode of a multitude of living creatures, each fulfilling its own biological destiny as best it may. Each has its own way of life, each inhabits its own private world. Each lives self-centredly—the other existences with which its own intersect are for the most part not even suspected. And yet the whole assemblage of lives is biologically entwined; it forms an interlocking whole.

In this little domain there live Mr. and Mrs. Everyman, with their son Master Everyman, one domestic servant, a tabby cat and a fox-terrier. Mrs. Everyman looks after the flowers, while Mr. Everyman makes himself responsible for the small vegetable plot at the far end of the garden. Here

also Master Everyman has a couple of hutches with tame rabbits.

Mr. Everyman is an active member of a large economic community. He goes off every morning to work or business. Mrs. Everyman is, as the phrase goes, " economically dependent " ; but she is the head of the little family world. The domestic life of the couple is on the whole exemplary—harmonious and agreeable. But Mr. Everyman finds it all but impossible to make his wife take an interest in business, while she finds him somewhat impervious in matters of dress and in local church affairs. The two get on very well together, but every now and then one of them is arrested before a gulf of incomprehension of the other's secret being.

As for Master Everyman, he is a source of mingled pride and trouble. Both his parents have really quite forgotten what it was like to be eight years old, and their idea of his private world, consisting as it does of a few meagre recollections, stuffed with rose-coloured retrospective sentiment, inflated with adult morality and with parental ambition for their offspring, is very far from tallying with the reality. He pursues his own way of life as best he may.

So does the maid. Mr. and Mrs. Everyman treat her kindly, but they do not make much of an effort to understand her peculiar inner life nor to discover how she spends her time on her evenings out. Her life is interlocked with theirs in a hundred ways ; but it remains intensely separate.

And when we come to the sub-human inhabitants the separateness and the mutual incomprehension increase. The Everyman fox-terrier is an affectionate dog, with the strong sympathy for his human master which so strangely characterizes the domesticated canine mind. He cringes to a reproof, is seized with tail-wagging at a cheerful word, and is thrown into a paroxysm of wriggling sentiment by forgiveness after a misdemeanour. But when he escapes from this human liaison, into what a queer diversity of existence he plunges ! An orgy of smells, a delightful rummaging in ordures, the

strange but rigorous canine social life with its olfactory etiquette.

The cat is even further removed from its human masters. It likes being stroked, but that is almost its only rapport. It is an alien being, with its slit-like eyes and nocturnal habits. It is perhaps most alien when, impelled by love, it howls and caterwauls upon the roof. But it exists always in a private world which only includes the Everymans in an objective, physical way.

A great part of its interest is concentrated upon the family stock of mice, who for some years have been established behind the wainscoting. Their life is a timid, twittering thing—pattering expeditions, lured on by good smells, out into the open kitchen or larder, with scuffles and rushes back into holes and the dark safety within. Puss meanwhile is wound up by the smell of mouse into a special feline activity—long periods of intent watching at holes, twitchings of tail, alertness to pounce.

The rabbits in the garden lead the most subordinate lives of all Mr. Everyman's hangers-on. Their very matings are controlled. What does Buck Rabbit think about it when he is ignominiously lifted by the ears and put, scuffling and kicking, with a doe he has never seen? We do not know. Probably he does not think about it at all. But he fulfils his biological duty, and presently there is a litter of little rabbits to continue the nose-twitching acceptance of cabbage-leaves in the back-garden hutch.

The cabbages are grown by Mr. Everyman in the plot near the rabbits. They are organisms, too. But if they have an interior world it is so dim as not to be worth bothering about, so vegetable as to be meaningless to an active animal organism like one of the Everymans.

Master Everyman was much excited last summer by finding a chrysalis on the fence near the cabbages. His father, quite correctly, told him it belonged to a Cabbage-White butterfly, and it was carefully put into a box and looked at every day. But instead of producing a butterfly,

the chrysalis became studded with a lot of little white cylinders, and out of each of these there hatched a lean and unpleasant-looking fly. Master Everyman was bitterly disappointed. He wanted to see the butterfly. It was no consolation to him that he had witnessed a remarkable case of parasitism. The flies were ichneumon flies. Their parent had laid its eggs in the white butterfly's caterpillar, and the grubs into which they hatched had devoured it from the inside.

Some years ago Mr. Everyman planted four little apple-trees at the end of the flower-garden, and now he is very proud because he gets seven or eight nice apples off each tree every autumn. He congratulates himself, but he forgets to thank the bees. If it were not for these pertinacious little creatures, which visit his garden every fine day from a hive over a mile away, his apple-blossom would not have been fertilized and he would have had no apples.

He is also quite oblivious of his other garden allies. He knows, of course, that there are plenty of fat, juicy earthworms in the soil he digs over: but, if he gives the matter a thought, he supposes that the benefit is all on one side, and that the worms ought to thank him for the provision of a home so admirably suited to their needs. Had he, however, read Mr. Darwin's delightful book on the subject he would realize that the benefit is mutual. The worms cannot thank him; they do not and cannot know of his existence. Even should he cut them in half with his spade, all they can know is the fact of the bisection. However, they pursue their own existence, and in the course of that existence they aerate the soil with their burrows, and help to drain it. They are all the time breaking the earth up into the finest soil as they eat their way through it and bringing material from the deeper layers to the surface in their castings. Mr. Everyman is at least aware of the existence of earthworms, but he does not suspect that in every ounce of soil there exist literally hundreds of millions of bacteria, and that on their chemical activities depends the fertility of his garden.

Nor does he know that this microscopic flora has its microscopic enemies. Prowling through the soil are innumerable small amœbæ which live on the bacteria. They are all aquatic, but they are so small that they can travel about comfortably in the invisible film of water which clings to every grain in ordinary moist soil: if the soil dries up, the bacteria and their enemies alike pass into a passive resting stage. He is quite certainly unaware of the fact, established by the Rothamsted Experimental Station, that the partial disinfection of the soil, or its partial sterilization by heat, will leave most of the bacteria alive but kill most of their protozoan enemies, and that this will promote fertility. If he had a greenhouse this fact might be of considerable importance; greenhouse soil often goes "sick," and it used to be the practice to throw it away and get fresh soil in. But we now know that the condition is due to too many protozoa and that killing them by heat will very cheaply restore the soil's fertility.

We must not forget Mrs. Everyman's pretty flowers. They charm the senses by their colour and smell—an apparently unnecessary gift of beauty; they appeal by their tender green and their punctual growth, their reachings upward to the light. The Everymans, however, have probably never reflected that the green is life's badge of factory labour, the outward and visible sign of an inward chemical grace; that the plants' ways of sprouting and growing have been imposed on them during evolution by the unceasing struggle for moisture and light, in which millions that did not come up to the standards of their environment have been ruthlessly massacred; and that the beauties of their flowers have a purely commercial basis as advertisement to insects. Taking this as a basis, man has stepped in and constructed biological monstrosities. Generations of gardeners and seedsmen have laboured to produce double flowers that are sterile because all their reproductive parts have been converted into mere showy petals; to manufacture plants, like many roses, that can only be con-

tinued by the unnatural process of grafting; to bring into existence delicate strains that would never have a chance in nature. In garden flowers man has taken beauties generated by hard necessity and distorted them to serve his own sensuous and emotional ends. Biologically speaking, garden flowers are parasites on the Everymans' æsthetic longings.

Besides the flowers there are the weeds. Ill weeds grow apace, and Mrs. Everyman often wonders why such nasty plants were created. But the weeds' extraordinary capacity for sowing themselves and coming up where they are not wanted is no less a product of struggle and selection than the colours of the flowers, and what are weeds in a garden are essential elements in natural vegetation. A bare patch on the face of earth is in a few decades covered with rich natural vegetation again; and what we call weeds are among the most important colonizers of unoccupied soil, preparing it for finer types, paving the way for the full climax of plant-life.

Nor let us omit the ubiquitous bacteria and moulds and other microbes. Their spores float in every breath of that air Mr. Everyman breathes, lie settled in every dusty corner. They turn his meat bad in hot weather, they sour his milk without a by-your-leave, they turn his bread mouldy if he leaves it too damp. A new strain of influenza microbes, started maybe in North-West Canada, or in Central Asia, sweeps across the world. The minute specks of disease-producing life infect Mr. Everyman as he travels to business; he brings them home and they pullulate in triumph through the bodies of his wife, son and servant.

And we had almost forgotten to tell you that the dog has worms; that introduces another large category of animals to add to this suburban menagerie.

§ 2

Habitats and their Inhabitants

All this variety of ways of living exists in one little patch of earth's surface. We must multiply it many thousandfold if we take in the whole earth, with all its innumerable habitats, from pole to equator, jungle to desert, high mountain to deep sea. The result is overwhelming: our minds cannot hold its abundance without the aid of some principle of arrangement. Confronted with the same difficulty when we set about the descriptive cataloguing of the many hundreds of thousands of living things, we found that a classification based on resemblance in structural plan brought order into the chaos. With this to guide us, we could pigeon-hole our creatures, could brigade them into groups, could systematize the crowd into an evolutionary army in which each had its definite place.

This we did by concentrating our attention on constructional plan and leaving way of life out of consideration. The fish-like whales and porpoises were put with the mammals, the snake-like slow-worm with the lizards. But every organism, if it must have its own plan of construction, must also live in its own way. And now the opposite aspect of the variety concerns us; we are interested in function more than structure, and are seeking a principle to help us classify creatures not by their blood-relationship but by their ways of life. What interests now about whales is not their past derivation from land-mammals, although this has left its impress indelibly upon their construction, but their marine way of life, and the fact that some are adapted to straining off tiny crustacea and molluscs from the sea-water, while others are fiercely and frankly carnivorous.

The simplifying idea which serves us here is also an evolutionary one. It is the idea of the moulding force exerted, directly or indirectly, upon the organism by its environment and its method of gaining a livelihood.

Life is often thought of as insurgent, a rebel rising against the limitations imposed upon it by outer nature and surmounting them. That is one aspect, and a very essential aspect of life. But if progress and the overcoming of difficulties by what we may metaphorically call biological invention are the cardinal aspects of life when looked at in the perspective of geological time, quite other aspects loom largest when we survey it as it is spread over the surface of the globe to-day. To such inspection, the main types of life—phyla, classes, orders—appear as definitely established and fundamental things; the rare "biological inventions" of life have taken place in the past and we take them for granted; what chiefly strike us in the present are the various ways in which these leading patterns have been adapted to different detailed conditions, the extraordinary plasticity of each of the main types of life's construction under the influence of different habitats.

In considering this plasticity and its results, there are two moulding forces which have to be taken into account. One is the effect of the organism's habitat, the other the effect of its way of life within that habitat. All animals and plants that live in the surface zone of the sea must in some way or other be able to keep themselves from sinking; all cave-animals must be adapted to darkness; all intestinal parasites to a shortage of oxygen. But in the surface layers of the sea one animal swims, another floats; one sifts and eats microscopic plants, another catches and devours large animals. In the intestine one parasite anchors itself, another wriggles freely about; one absorbs ready-digested food, another eats it when only half-digested. Our first and main simplification will be to divide the realm of life into a number of habitats, each with its own distinctive conditions; and then to study the way in which the animals and plants have become adapted to these conditions—in brief, how the habitat moulds its inhabitants.

Besides this, we shall also have to take some account of the different ways of life possible within each habitat, and

see how they too mould the creatures which adopt them. But different ways of life are linked together. Carnivore eats herbivore, herbivore eats plants, plants live largely on the products of animals and their decay. Brought back from a contemplation of the variety of life to its inter-relations and to its unity, we shall find ourselves devot[ing] the concluding chapters of this volume to what we [may] call the Economics of Life, the science of vital interconnections which is termed Ecology. But our first business is to set forth some of the varied spectacles of life that are revealed as we pass from habitat to habitat.

It is true that the biosphere, as the life-inhabited zone of earth is sometimes styled, is a mere skin. About ninety-nine hundredths of living things are crowded into a "life-skin" not more than a thousandth of the earth's radius in thickness, and occupying about one-third of one per cent. of its volume. Such a skin on a regulation-size Association football would be less than $\frac{1}{200}$ of an inch thick. Even if we take in the rare extremes, this thickness need only be multiplied by four or at most five. In spite of this, the biosphere skin is extremely varied in the homes it offers to life. There are first the differences in medium—air, earth, water; differences in salinity from almost pure water to the Dead Sea's more than twenty per cent. of salts; differences in temperature from hot springs that are nearly boiling, down to many degrees below freezing; differences in pressure from well below half an atmosphere on high mountains to several hundred atmospheres in the deep sea; differences in light from the intense tropical sun to the utter darkness of caves, of the oceanic abyss, or of an animal's gut. And all these various differences of temperature, light and pressure, of climate and situation, may be combined in an almost bewildering multiplicity to give the actual habitats in which animals and plants live out their lives. Of these we need not here give any detailed or formal classification; but before we go on to description, it will be as well to remind ourselves of the chief kinds of habitats available for life.

The original home of life was water—sea-water. The whole of the sea is inhabitable, both the firm bottom and all the vast succession of layers of open water in which life must float or swim.

As the shore is approached, and the influence of the tides and the waves is felt, conditions change, and a multiplicity of new habitats are provided. Climate too makes itself felt; there are no coral reefs in the arctic. And here and there special conditions make special habitats, such as that weedy Atlantic slackwater known as the Sargasso Sea.

Then there is brackish water, bridging the gap between the habitats of the sea and of inland waters. Inland waters, in spite of their small extent in comparison with the sea, provide an amazing diversity of habitats. There are salt lakes far saltier than the sea, there are almost saltless rivers. There are hot springs, and arctic waters that spend most of their time as ice. There are running waters of all degrees of turbulence, and there are deep and quiet rivers. There are lakes big enough to be oceans in miniature, with their own deep-water unilluminated zone and their various layers of free-floating and free-swimming life. And from these huge bodies of water there is every gradation down through ponds and pools, to temporary puddles, to the Lilliputian lakes that collect in the hollows of old trees, and to the mere films of water on leaves or sticks or between grains of soil, that can still harbour microscopic swimming life.

As lagoons and estuaries connect the worlds of sea- and fresh-water, so the worlds of water and land are connected by the transition zones of shore, of temporary pools, of swamps and marshes and mud-flats; and all these linking habitats will be differently populated according as they are fresh or salt.

The habitats provided by land are perhaps the most varied of all. There is the strange world of the soil itself, comprising the animals and plants wholly or mainly confined to a life below ground, embedded in or burrowing through the earth. But the greater number of land-habitats

differ profoundly from those of water in being practically restricted to two dimensions only, spread over the surface that divides earth and air. Aquatic life exists in three dimensions; land-life is like a film. The inhabitants of this surface zone differ according to climate far more than do those of the sea, even of the sea's surface. So far as land-plants are concerned, climate is the overruling factor, and any broad classification of their habitats must be drawn on climatic lines. We have arctic habitats, sub-arctic, temperate, sub-tropical and tropical; besides these zonal divisions, there are divisions according to altitude—plain, hill and mountain. Finally, these habitats can be further classified according to soil conditions.

With land animals, on the other hand, habitats are more an affair of the environments provided by plants; the influence of climate upon them is at one remove.

One important animal habitat, for instance, is the arboreal; the modifications induced by living in trees are more striking than those related to the climate in which the trees happen to grow. In forests, especially tropical forests, animal as well as plant life is stratified in horizontal layers, almost as in the sea; there is the tree-top layer, several layers in the less well-lit habitat of the region below the tops but above the ground, and the ground-layer between the trees.

The characteristic vegetation of steppe, savannah and tundra is the chief agent in making of each of these a distinct animal habitat; and the very absence or limitation of plant-growth in deserts is one of the characteristics most important for their animal inhabitants. Caves afford a minor but interesting habitat to land and to fresh-water life; and another peculiar habitat is that now provided by man, in his buildings and yards, his fields and gardens, to special types, like sparrow and cockroach, that can take advantage of the opportunities so richly provided there.

Air as a habitat is in a certain sense less important than either earth or water, since no organisms inhabit it per-

manently, but only between terrestrial or aquatic interludes. Nevertheless, it exerts a potent moulding force upon the creatures who have taken, however temporarily, to existence in its medium, and may properly rank as one of the larger habitat divisions of the earth. The less temporary and occasional, however, is the stay of a creature in air, the less does any subdivision of aerial habitat become possible for it; and it is symptomatic that the greatest mobility and range over the earth's surface found in any non-human species occur in the birds. This is, if you like, the obverse of the fact that the only satisfactory classification of flying creatures is by the habitats they frequent when *not* in the air—water-birds and water-insects against land-birds and land-insects, and so on.

There remains one further major type of habitat, which is neither earth, air nor water, but rather fish, flesh or fowl; it is the habitat provided by the living bodies of other creatures and occupied by the horde of parasites. It is a habitat within a habitat: none the less, its moulding effect on its parasite inhabitants is striking in the extreme. And in variety it does not yield to any other main kind of habitat. A parasite may be external or internal: it may live in or on an animal or a plant: it may inhabit blood or muscle or intestine.

The common frog is an excellent example of their variety and abundance: it is a little zoological garden of parasite life. Besides various kinds of bacteria in its gut, every specimen harbours a swarm of big ciliate protozoa of several kinds in its rectum, a roundworm and a fluke in its lungs, more flukes in its bladder. Sporozoan parasites are common, flagellates occur regularly, fungi may attack the skin, and there are literally dozens of rarer parasites of various kinds.

The world of parasites is a major world of life, worthy to rank with the worlds of sea, of fresh-water and of land in the number of its inhabitants and the variety of their ways of living.

§ 3

Ways of getting a Living

In each habitat, different organisms live in different ways. One takes advantage of one set of opportunities which the habitat provides, another of others. Different creatures surmount the same difficulties by different methods. Accordingly, even in one and the same habitat, there will be many modes of life. The modes of life hinge first upon food, and then upon reproduction. And since the verb *to eat* is conjugated by life as much in the passive as in the active, modes of life in relation to food will include not only modes of feeding but modes of avoiding being fed upon. In this section, however, we shall illustrate our point with reference solely to ways of feeding.

The first great division in regard to feeding is that between green plant and animal. The green plant, strictly speaking, does not feed at all; it makes its own food inside the living factories of its cells, taking in the simple raw materials it needs from the inorganic medium in which it lives. The animal, on the other hand, can only utilize carbon and nitrogen in ready-made organic form; it profits by the green plant's labours.

There are also subsidiary modes of plant nutrition, such as that of most fungi, which need organic compounds, but of a much lower complexity than those required by animals; and the special modes of nutrition possible to nitrogen-fixing and other forms of bacteria. Every group of plants has also its parasitic representatives, and in the flowering plants there are some which are "carnivorous."

All animals, on the other hand, get their food either directly or at one or more removes from green plants. The usual division is into herbivores and carnivores, but perhaps the best classification is into what may be called micro-feeders, which live upon relatively minute particles, engulfing them without any selection, and macro-feeders, which

usually select their food, and in any case take it in relatively large portions.

The word *relatively* is used of set purpose. A whalebone whale swims its devouring way through swarms of little crustacea or butterfly snails, taking 10,000 at a gulp. It is obviously using a micro-feeding method; yet one of these identical molluscs or crustacea, if captured individually by a small fish or medusa, would be a victim of macro-feeding.

The most general method of micro-feeding is to produce a current of water, usually by means of cilia, and then to sift out the contained food-particles from the current by some mechanical device. This is adopted by all sponges, sea-squirts and bivalve molluscs, many worms, Polyzoa, and other forms, including Amphioxus. The other main method is based upon chemical instead of mechanical sifting. The animal, instead of passing a current of water over its tentacles or through its gills, eats its way through its sandy, earthy, or muddy surroundings, and forces a column of the unpromising material through its tubular gut; the digestive juices dissolve any nutrient matter present, and this is then absorbed, while the remainder is passed out at the anus. This is the method of earthworms, lugworms, Balanoglossus and heart-urchins.

The essence of these micro-feeding methods is their automatic nature; the animal does not in any way select its meal, but its food is simply filtered or digested off from the liquid or solid medium in which it happens to lie. Occasionally, however, some selection enters in; herrings and whales choose patches of sea rich in plankton, and some of the sand-eaters appear to reject certain types of particles.

In general, however, all is grist that comes to the micro-feeders' mill, and they are essentially omnivores. If some, like whales, are predominantly animal-eaters, and others, like the minute Tunicates known as appendicularians, predominantly vegetable-eaters, this is an accident, determined much more by the size of the organisms eaten than by their vegetable or animal nature.

Macro-feeders, on the other hand, often show more specialization in their food. Since they take large mouthfuls, they need different kinds of mouths and teeth for animal and vegetable food, and, still more important, very different arrangements are required to catch and hold an active animal from those needed to browse upon stationary and unresisting grass or trees.

Vegetable macro-feeders, however, if less interesting in regard to their methods of securing their food, show numerous adaptations for its proper utilization. In the first place, the nutritious parts of green plants, the cell-contents, are all shut up in their little cell-wall boxes, made of cellulose (or even of wood), which is as indigestible to almost all animals as it is to us. A vegetable-feeding animal with no device for breaking open these microscopic boxes would be just as helpless as we are when all we have to eat is a box of sardines and we have lost the opener.

The usual method of box-opening is mechanical trituration; this may be done by rasping organs, like the radula "tongue" of snails, or by regular grindstones of teeth, as in a cow or an elephant, or by grinding gizzards, whose grinding power often depends on sand or stones deliberately swallowed, as with many birds. In addition, bacteria may be enlisted to break up the cellulose chemically, as in the gut of many hoofed mammals.

Owing to the bulk of cellulose, and the need for time to dissolve out the contents of the cell-boxes, the gut of herbivores is, almost without exception, relatively longer than that of carnivores, and often provided with voluminous outgrowths (like the cæcum in a rabbit, for instance), in which the food may be stored while it is exposed to bacterial action (Fig. 1).

Most herbivores eat the green parts of plants, and may be roughly divided according to their method of eating. There are grazing types, whose green food, often relatively small, is spread out over a surface; examples of these are sheep, fresh-water snails, and those small caterpillars which

merely eat away the surface of the leaves over which they crawl. The browsers, on the other hand (though there is every intermediate gradation), in general take portions from larger plants. There are fishes that bite pieces off the large seaweeds; giraffes and most deer browse off trees; many caterpillars take respectable mouthfuls out of the edges of leaves. Finally, there are the miners and borers, so small in relation to their food that they live not merely on but in it. The leaf-mining caterpillars and grubs of various moths and beetles are the best known examples. These eat their way through their environment just as do the sand- or mud-eaters; but what the herbivorous miners eat is all food, while the food of the soil-eater must be digested out of a mass of unnutritious material.

Besides the main type of green-eating herbivore, there are vegetable-feeders adapted for eating other parts of plants—fruits, seeds, bark (including even cork), wood, roots, tubers, the sap, special secretions like nectar, and even the pollen. In many cases the smaller animals live *in* their food, the large come and bite it off. There are, for instance, plenty of fruit-inhabiting and grain-inhabiting insects, as well as animals which eat fruits or seeds in a more ordinary way, such as toucans and fruit-bats on the one hand, finches, nuthatches and harvester-ants on the other; and there is even a Malayan squirrel which, after gnawing a hole in a coco-nut shell, gets right inside for the business of eating.

Among carnivore macro-feeders, there are as many adaptations as among herbivores. The tearing and cutting teeth of wolf or tiger are but one type. The teeth of some rays are turned into shellfish-crushers; of various bony fish into beaks for biting off coral. Whelks bore holes in the shells of their bivalve prey. Snipe and woodcock have beaks converted into sensitive and flexible worm-detectors and pincers; those of herons are converted into fish-spears, of hawks and owls into flesh-tearers. Ways of life are as multifarious as habitats; and both set their stamp upon living creatures.

§ 4

The Adjustment of Inhabitant to Habitat

It is an obvious fact that on the whole animals and plants fit their surroundings; there is a definite correlation between the peculiarities of inhabitants and those of habitats. A

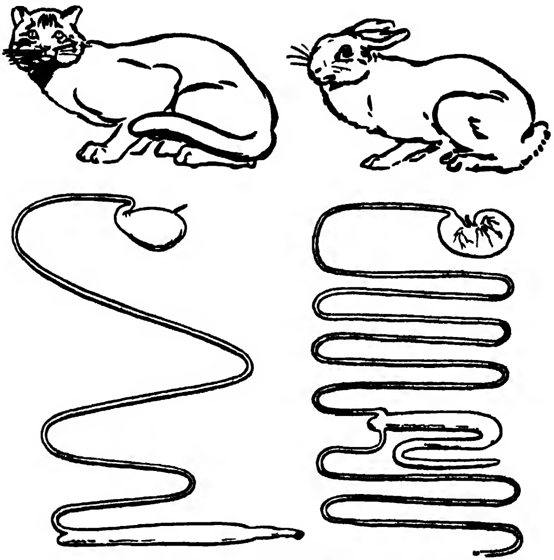

FIG. 1.—ADAPTATION TO DIFFERENT KINDS OF DIET.

A cat and a rabbit of the same weight, with their stomach and intestines on the same scale. Note the big blind-gut or cæcum of the rabbit.

few examples will illustrate the point better than pages of generalities. In the high northern latitudes, white birds and mammals occur in far larger proportions than elsewhere; while in deserts the preponderance of buff, fawn and sandy-coloured animals is equally noticeable. Or again, an unusual percentage of the inhabitants of the surface

layers of the ocean possess one or more of the following peculiarities, which are rare elsewhere—either glassy transparency or else blue colour; long, projecting spines or flaps; bell-shaped construction. Below about a hundred fathoms, on the other hand, the majority of animals are either black or red (both colours being uncommon in most other parts both of sea and land) and possess luminous organs; and their eyes are either abnormally large or else abnormally small or absent.

The preponderance of deciduous, non-coniferous trees in the temperate zone, of evergreen conifers in higher latitudes and on mountains, and of evergreen non-coniferous trees in tropical forests is a good example of correlation of flora with environment; and the unusual abundance of succulent plants in deserts and near the sea is another.

Half a century ago, almost everyone would have unhesitatingly accepted such characteristics as adaptations which in some way conferred biological advantage upon their possessors. But there has been a reaction against a too facile application of Darwinian principles, and nowadays it is realized that there may be other interpretations for such facts as these.

As an example, let us take the similarity of the colour of desert animals to their surroundings. This is often very marked; and the older naturalists presumed that it had arisen through its conferring on its possessors a cloak of comparative invisibility. Later students of the problem, however, like P. A. Buxton in his *Animal Life in Deserts*, point out a number of difficulties. The most striking, perhaps, is that a number of desert animals which are wholly nocturnal, and therefore, one would think, can receive neither benefit nor the reverse from their coloration, are yet of this same sandiness of colour. He therefore concludes that one or other of the conditions of desert existence must act more directly upon the desert's inhabitants, forcing them to become sandy, whether it is advantageous or not. There is, in fact, as J. A. Allen long ago pointed out, a

frequent geographical correlation of a more general nature than that between deserts and sandy colour, namely, a gradual darkening of the colour both of mammals and birds with humidity, a lightening with aridity; and it might be supposed that the amount of water-vapour in the air directly influenced colour. As further complication, however, desert creatures closely related to sandy-coloured species (and this occurs among mammals, birds and insects) may be very conspicuous, black being a frequent colour; and yet such animals seem to be just as successful as their inconspicuous relatives.

There the problem stands. Upholders of the theory of adaptation will urge against Buxton's views that, in the brilliant atmosphere of the desert, it is just as important for an animal to blend with its surroundings on a moonlit night as it would be by day. And the supporters of the "direct action" view must, of course, admit that even if light sandy colours were first produced as the result of aridity (or some other condition of desert climate), with no reference to their biological value, yet when produced they would be likely to have biological value for many species, and would therefore be perpetuated. Their concealing qualities could later be perfected by Natural Selection if appropriate mutations turned up.

The temptation to interpret the facts in terms of the inheritance of acquired characters is a strong one. It is true, as Beebe showed, that in some species humidity and aridity have a direct effect upon the colour of individuals. This is so, for instance, with the dove, *Scardafella inca*, which when kept in a very moist atmosphere gradually assumed the dark colour characteristic of the sub-species found naturally in moister climates. But in certain other examples, such as the American deer-mice of the genus Peromyscus, the case is different. The various sub-species of the common Californian deer-mouse show a considerable degree of parallelism between their coat-colour and the prevailing colour of their surroundings, the sandy tone of

those from arid habitats being very noticeable. But when these were bred by Sumner under experimental conditions, he found that the characteristic colours of the fur persisted unchanged in spite of quite new conditions of temperature and moisture. In other words, we are presented with the phenomenon of a visible character having sometimes to be produced afresh in each generation as a response to environmental conditions, in other species being produced in all kinds of conditions owing to hereditary factors.

The problem can only be solved by new observations and new experiments. The question whether such habitat-correlated characters are advantageous to all or to some of their possessors can only be settled by intensive work in the animals' natural surroundings; while, whether they are useful or not, the question as to their method of origin—by modification in each generation, by Lamarckian means, by induced mutations in the germ-plasm, or by random variation guided into certain channels by Natural Selection—can only be settled by a painstaking combination of physiological experiment and breeding tests.

Moreover, there is an important theoretical consideration that has often been overlooked. An adaptive character may give its possessors a definite advantage over other members of the species, and so in the course of generations automatically become a character of all the members of the species; and yet it may confer no advantage upon the species as a species. This principle of what is called intra-specific selection is very possibly applicable to the persistence in deserts of sandy-coloured and conspicuous animals side by side. If variations crop up in the direction of sandiness and consequent concealment, they will gradually oust the other colours of the species. But if they do not, some species may persist quite happily in spite of conspicuous colouring.

In general, however, it must be admitted that probably the great majority of these correlations with habitat are adaptive; the most reasonable explanation at present is

that they have arisen under the guiding action of Natural Selection. The existence of the same type of structure or habit in a number of different species in one habitat is not only an interesting fact, but it also constitutes *prima facie* evidence for the adaptive nature of the structure or habit in question; and when we can reasonably interpret the structure or the habit in an adaptive way, though we are not thereby exempted from the duty of putting our interpretation to more decisive tests, we are justified in so doing as a working hypothesis until evidence to the contrary is forthcoming.

Accordingly, what we shall do in the following pages is in the main to illustrate the intense variety of living things by pursuing life through a variety of habitats. We shall also point out those peculiarities which seem to fit the inhabitants to their surroundings; but we shall not attempt to discuss the evolutionary origin of these adaptations.

CHAPTER II

LIFE IN THE SEA

§ 1. Life in the Sea. § 2. The Surface Life of the Sea. § 3. The Deep Sea. § 4. On the Floor of the Abyss. § 5. Seashore Life. § 6. Coral Reefs and Islands. § 7. Holes and Corners of Sea-life

§ 1

Life in the Sea

THE sea provides a vastly greater space for life to inhabit than does the land. Not only does it extend over more than two-thirds of the surface of the globe, not only does it lack all blank lifeless areas such as are found on land in the Antarctic ice-cap or the tops of the great mountain ranges, but it is inhabited in three dimensions. The average depth of the sea is somewhere about 12,000 feet, and all of this vast body of water (save possibly a few of the deepest pockets) has its inhabitants. It is true that below the limits to which light penetrates the sea's population is sparse; but even so, it is richly inhabited to a depth of 150 to 200 feet, and inhabited by a wonderful multiple population, layer below layer, each layer different from its neighbours.

And yet the number of kinds of creatures that live in it is very much inferior to the number of kinds that live on land. The last time that a detailed analysis was made (in 1898) only 85,000 species of aquatic animals—and this is including the fresh-waters with the sea—were on record, as against 327,000 land-animals. The difference was doubt-

less due in part to the greater attention paid to the inhabitants of the land; but in spite of this factor the comparative richness of the land-fauna cannot be denied. This paucity of species is apparently a direct result of the much greater uniformity of conditions in the sea. Nor is there any isolation of one part of the sea from another as there is between bits of land or bits of fresh-water; it is a well-known empirical fact that isolation helps to generate new types.

But this numerical poverty is offset by the greater variety of the main types of construction; marine life may be said to ring fewer variations, but on more themes. Not one of the phyla of animals but has some marine representatives. A few classes of animals, notably the amphibians and centipedes, are altogether absent from the sea, and the biggest class of all, the insects, is extremely scarce in salt-water. But there are whole phyla of animals which are only found in the sea, like the lampshells and the echinoderms, and others, like the sponges and the cœlenterates, which are almost all marine. Besides this there are many classes of the larger groups or phyla that include sea-animals only, such as the cephalopods, in some ways the most highly developed of invertebrates, the sea-squirts, the radiolarians, amphioxus and its relatives —indeed, over a third of the number of animal classes that are recognized by zoologists.

The explanation of this variety of type is doubtless an historical one: life originated in the sea. In this spacious home, life, evolving through long epochs, branched out into a great number of types, some lower, some higher; but only a few of these succeeded in making the advance into fresh-water or on to land.

* * * * *

Sea-life is unlike land-life not merely in the strange and varied types of creatures that enjoy it, but in other more fundamental ways. Shelley vividly pictured its lovely profusion. Listen to him as he speaks of the West Wind:

Thou who did'st waken from his summer dreams
  The blue Mediterranean, where he lay,
Lulled by the coil of his crystalline streams,
  Beside a pumice isle in Baia's bay,
And saw in sleep old palaces and towers
  Quivering within the wave's intenser day,
All overgrown with azure moss, and flowers
  So sweet the sense faints picturing them ! Thou
For whose path the Atlantic's level powers
  Cleave themselves into chasms, while far below
The sea-blooms and the oozy woods which wear
  The sapless foliage of the ocean, know
Thy voice, and suddenly grow grey with fear,
  And tremble and despoil themselves: O hear !

Sea-life is as intense and as beautiful as he imagined it. But there are no flowers and no woods: save in parts of a zone of shallow water round the coasts, the sea-bottom grows no plants. The great bulk of the "meadows," "shrubberies" and "forests" of the ocean are animal in nature, incapable of making their own nutriment. Even when rooted, stalked, branched, and to a casual glance completely plant-like, the growths on the sea-bottom are without leaves or flowers. Their branches and stems are hollow, so many stomachs; they are studded with greedy mouths: and they owe their flower-like appearance to the cruel tentacles which bring about the capture of prey by snare or microscopic swirl.

None the less, the green plants are there: they must be there, or the sea could not support life. If green plants are to exist in the sea, they must live in the light: and light is gradually absorbed as it passes through sea-water. Not only will nearly all the ocean floor be dark, and uninhabitable by green plants, but even in shallow waters, where light can reach the bottom, there will be more light at the surface. The great vegetable-garden of the sea is its top layer of water, some fifty yards deep. All over the watery surface of the globe, even in the middle of the greatest oceans, there is this upper layer of water that teems with green productive life.

Plants growing in this marine meadow need no absorbing roots and no strong supporting stem; but they must float.

If they were large, they would need to be kept from sinking in some way, as by gas-bladder floats. But the most economical solution of the problem is to remain microscopic. A given bulk of plant-tissue divided up into small single cells

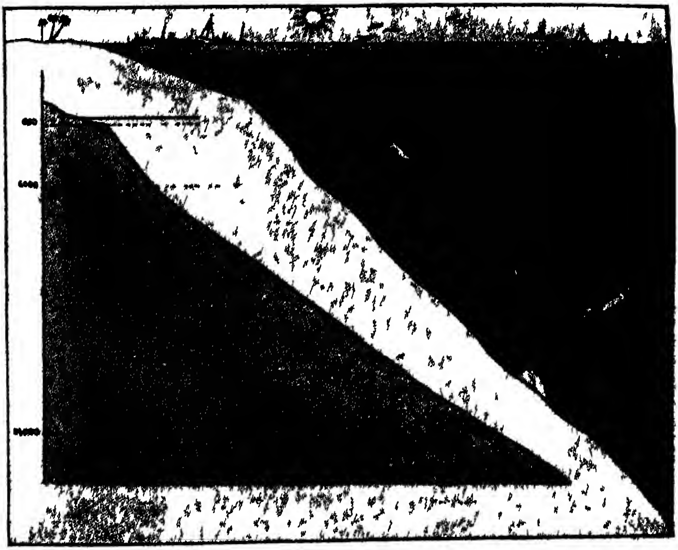

FIG. 2.—A DIAGRAM OF THE ZONES OF THE SEA.

The sun helps the seaweeds and microscopic sea-plants to build up living substance. They feed the sea-animals. Light sufficient for abundant plant-life penetrates to about 200 feet; practically no plants are found below 600 feet. The creatures in the blackness of the deep sea are all animals dependent on a food-rain from above. The sea-bottom usually slopes gently at first to the edge of the continental shelf, then dips steeply to about 6,000 feet, then more gently to the abyss, little of which is over 24,000 feet deep. In the main diagram, the upper zones have had to be exaggerated; the true depth scale is shown in the inset.

will possess a far greater extent of surface than if combined into large plant-bodies. The increased surface will have two advantages. It will allow the maximum utilization of light and of the dissolved salts of sea-water, for each cell will be

illuminated and bathed on all sides, and there will be no need of transport-systems within the tiny body; and, since frictional resistance to sinking through the water increases with the increase of surface, small units of life can keep up in the water much more easily than large, and need not have recourse to special floats. The union of a thousand million cells would only make a very small bit of seaweed. But the proportion of surface to bulk in this would be only about one-thousandth of what it would be in each cell if they had all stayed separate.

The floating inhabitants of open water are collectively called the *plankton*—"that which is drifted about." Plankton is another of those technical terms which sooner or later will fix themselves into common speech; for it constitutes the main food-supply of the sea. Almost the whole of sea-life is nourished by the plankton. Plankton is the base of the sea's vital pyramid, on which are supported almost all our food-fishes, and even the great whales.

The microscopic plants of the plankton are mostly of two types, diatoms and flagellates. The larger flagellates belong for the most part to the curious-looking group called Dinoflagellates, while many of the smaller belong to the equally curious group of Coccolithophoridæ.

In certain spots, at certain times, the crop of plant-plankton is so dense that it discolours the sea over large patches. But for the most part the plantlets remain invisible and unsuspected until tow-net and microscope are brought to bear. Even with the aid of the finest silk tow-net, however, many of the smaller floating plants are never captured; and only in the last few years has Lohmann discovered the extraordinary abundance and importance of this dwarf plankton or *nanno-plankton.* In part he obtained his knowledge by centrifuging large volumes of surface water, and examining with a microscope the fine sediment thrown down; in part he utilized the collections made by some of nature's tow-nets—the filtering and straining apparatus of small ciliary feeders like Appendicularia (a free-swimming relative of the Sea-

squirts), compared to which the meshes of any tow-net would look like wire-netting, for they catch objects down to 3μ across, and exclude everything over 20μ ($1\mu = \cdot 001$ mm.).

A great deal of work has been done in the last fifty years upon these tiny creatures; and as a result we are beginning to know something about their distribution, their habits, and their multiplication.

There is an orderly succession of different kinds of sea-drifting creatures through the year, just as there is an orderly succession of the growth and flowering of plants in a wood. In spring, the diatoms and other tiny plantlets begin to multiply; following on their heels come swarms of small animals, mainly larvæ which bottom-livers send up to take advantage of the diatom harvest; and their abundance is the cause of multiplication of larger and carnivorous animals. The plankton is at its richest in late spring; by then the burst of plant-growth has exhausted most of the available nitrates and phosphates, and the surface-zone must wait for a new quickening until the winter cools the top layer of water. The cold water is heavy and sinks: unexploited water, rich in nitrates and phosphates, rises from the depths to take its place; and the cycle can begin again as soon as the temperature rises high enough.

And there is an orderly distribution of the plankton over the roof of the sea. For chemical reasons, certain salts needed as plant-food are more abundant in cold than in hot water, and so plankton and surface life in general is more plentiful at either end of the globe, less plentiful round its middle. This regularity is interfered with by currents; the Gulf Stream flows on the surface right up to the coasts of Spitsbergen, but then sinks below the polar water, which is less salty because of melting ice, and plunges downwards; thus we may find warm-water forms descending to an inevitable death, deep below the pack-ice of the arctic sea. The antarctic current brings cold water and rich life far up the west coast of South America. One day the life of the world's seas will be properly explored; and then we shall be able

to chart them, season by season, according to the abundance of their basic food-supply, the plankton. A promising beginning has been made with the Atlantic.

Naturally this rich marine meadow is pastured by swarms of animals, but, owing to the microscopic size of its constituent plants, no large animals can browse directly on the vegetation; there are no creatures of the open sea corresponding in their diet to cow or deer, elephant or hippopotamus, or even to rabbit or prairie-dog. All the herbivores here are small, often indeed minute, and constitute only the first links of the food-chains which culminate in whale and dolphin, bonito and mackerel, argonaut and giant jelly-fish. This absence of large plant-eaters from the sea meant that all the fishy ancestors of the land-vertebrates, and therefore the earliest land-vertebrates themselves, were carnivores. So the moulding effect of the environment radiates out from its original centre, affecting one remove of creatures after another and extending its influence even into another habitat. Who would have imagined that the predominance of flesh-eaters among amphibians and the earliest reptiles was a consequence of the necessity that sea-plants should be microscopic in order to float the better? Yet so it is.

§ 2

The Surface Life of the Sea

When Mr. Everyman takes his family to the seaside, and they all adventurously go out in a rowboat, they little suspect, as they look over the gunwale, how full of life are the blue-green, choppy waters around them. They could gain an idea of this abundance if they provided themselves with a tow-net—a long conical net of fine muslin, or better, of bolting-silk of the sort used by millers to sift flour, to whose end is tied a glass or metal container. If this be towed patiently behind a boat for half an hour or so at slow rowing speed, it will collect a fair sample of the sea's surface

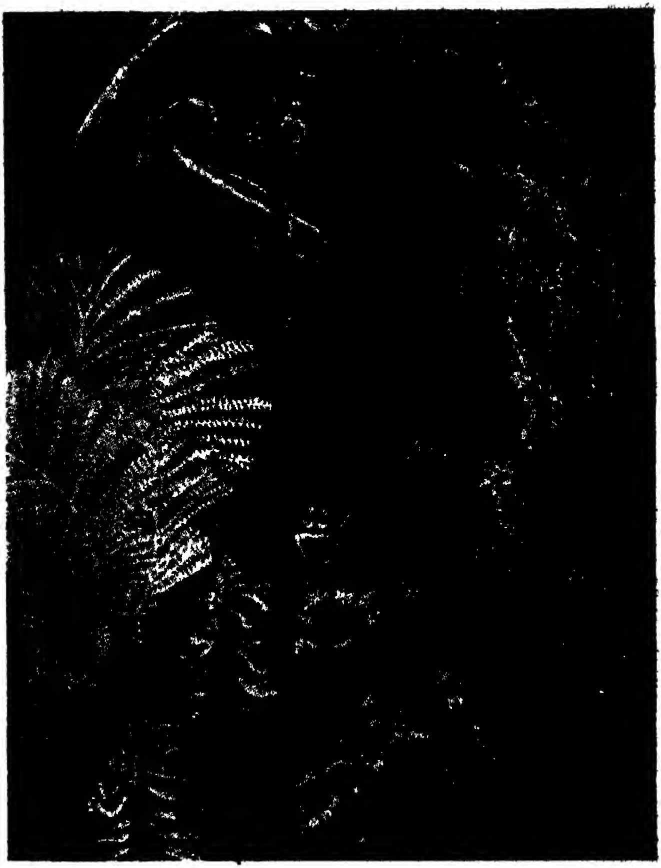

FIG. 3.—AN ANIMAL FOREST—A SCENE AT A MODERATE DEPTH ON GRAVEL BOTTOM.

Colony-forming cœlenterates studded with polyps are the most prominent forms of life: sea-fans on the left, tall Alcyonarians centre and right, sea-pens in the foreground. In the middle distance are sea-anemones and corals. Fish and a spider-crab complete the picture.

(Based on an exhibit of animals collected by the "Discovery" Expedition, in the Natural History Museum, London.)

inhabitants. Take the sample home and look at it under a low power of the microscope; a new and strange world of life is revealed. If you have chosen locality and season well, the variety of creatures will be extraordinary. Here are abundance of crustaceans, rowing themselves along by means of their long antennæ. Some of them are adult and spend all their lives thus constantly active in the roof of the sea. Others are the babies of bigger bottom-dwelling creatures—crabs, lobsters, prawns, barnacles—which spend their larval existence here before sinking to the bottom. It is these immature larval forms which make up the great majority of this population (Fig. 4).

For the surface zone is the sea's main nursery. Drawing their nourishment either directly or indirectly from the minute plants of the plankton, the tiny glassy creatures can feed and grow here until they are big enough to cope with the different methods of feeding imposed by larger size and crawling life. There are fish eggs buoyed up with floats of oil, which presently hatch out into glassy fishlets, often amazingly different from their future adult selves. There are larvæ of sea-urchins and brittle-stars, looking rather like a painter's easel turned upside down, larvæ of starfish and sea-cucumbers, perhaps of sea-lilies; the "wheel-bearer" larvæ of bristle-worms and of molluscs, often curiously alike, with a wheel-like girdle of big cells carrying strong cilia. Later on some of the mollusc larvæ grow tiny shells and a rudimentary foot. There are larvæ of sponges and polyps and jelly-fish, of sea-mats and other Polyzoa, and the microscopic tadpoles that later degenerate and grow into sea-squirts.

The sea's nursery has its drawbacks. Of these millions of marine babies, only a minute fraction survives. If you send forth your new-hatched young unprotected into the world, you must expect a massacre of the innocents. They fall a prey to all kinds of small carnivorous creatures, glassy like themselves. Among these are the arrow-worms, rapid swimmers with cruel biting mouths; battalions of jelly-fish of every size, trailing their paralysing net of tentacles; and

Ctenophores (comb-jellies) whose tentacles capture not by their poison but by their adhesiveness.

There are swifter and larger creatures too who profit by the abundance of surface life, like the mackerel who strains off the plankton from the water-current through his gills; but these of course will elude your tow-net.

Then of single-celled creatures there is a great abundance. Our temperate waters on summer nights may come alive with pinpricks of light; these are produced by the swollen spherical protozoan Noctiluca—"Shine-by-Night." Of the innumerable single-celled plants we have already spoken. Single-celled animals are not so abundant inshore; but far out in the ocean the open water is full of Radiolarians of strange and delicate construction, together with some floating Foraminiferans. And these creatures are mostly so small and so transparent that men pass through the midst of them without even realizing their existence. Yet it is they which make our fisheries possible.

In this section we shall consider mainly the well-lighted surface zone of the open sea, which is the prime generator of food for the whole ocean. But first we must introduce a couple of technical but necessary terms. All the open waters taken together make up the *pelagic* or open-sea zone; here life must either float or swim. All the bottom constitutes the *benthic* zone, where crawling or burrowing or fixed attachment becomes possible. Both zones are to be divided again, according to depth, into the well-illuminated zone and the deep-sea or *abyssal* zone of darkness, with an intermediate twilit layer between. And both can be divided, according to their approach to land, into the *littoral* zone round the shore, and the great bulk of the waters, the high seas, outside.

The first need for the inhabitants of the surface zone is not to sink, not to lose contact with the light. Some creatures float passively. Others, which we may call the passive swimmers, make movements not to get anywhere in particular, but merely to keep up in the water. The more active swimming

of still others serves not only to prevent sinking but to generate a food-current to be sifted. And finally there are the creatures which swim actively and deliberately seek their prey. Some of these, like the arrow-worms, are microscopic, but the larger, like whales and most fish, are big enough to be able to set currents at defiance and migrate from place to place. These last are sometimes spoken of as the true active swimmers, while all the rest make up the drifting plankton.

The plants of the sea are not nearly so passive as those of land. The diatoms of the plankton merely float; but the dinoflagellates and many others use their flagella actively and incessantly to help keep up in the water. The dinoflagellates and the diatoms also illustrate a common anti-sinking device, the increase of the amount of surface relative to weight; in their case this is achieved by long spines into which their body is drawn out. It is the same adaptation that gives so many crustacean larvæ their grotesque and gnome-like appearance (Fig. 4). In other pelagic creatures, the same end—increase of surface—may be attained in a variety of ways: by protruding spines or feathery hairs, by projecting planes, by a flattening of the whole body, or (combining surface-increase with muscular movement) by construction in the shape of a bell. And any of these devices may be combined with others for reducing specific gravity. The bell-shape is of course common in jelly-fish. But it is equally marked in many pelagic cuttle-fish, and in the only pelagic sea-cucumber Pelagothuria.

The illustration, Fig. 5, will show some of the fantastic forms produced by the need for spines or planes. In some copepods resistance is effected by branched hairs which have developed an extraordinary resemblance to feathers, both in appearance and function, although their branches do not interlock.

The saltness of water and still more its coldness increase its viscosity, and therefore its resistance to objects sinking through it. This physical peculiarity of the environment is reflected in the most delicate way in the anti-sinking

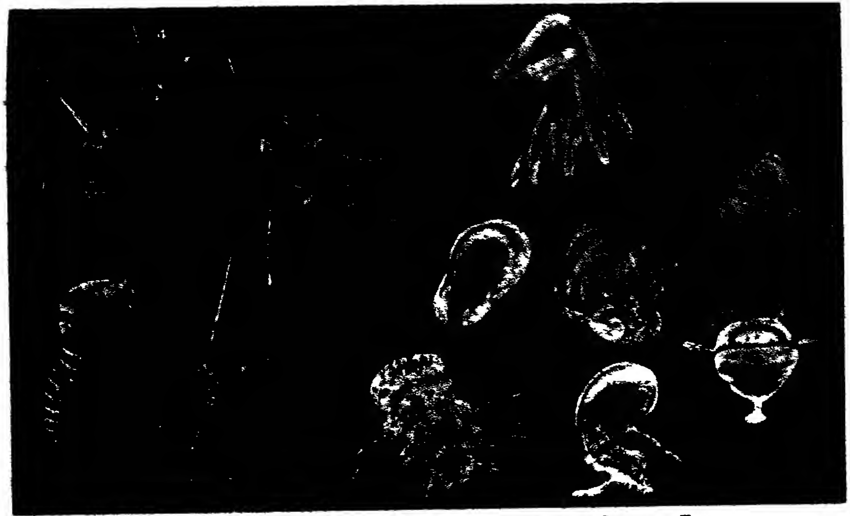

FIG. 4.—SOME FREE-SWIMMING LARVÆ OF THE SEA'S SURFACE ZONE.

(1) The Pilidium larva of a Nemertine worm. (2) The Trochophore larva of a primitive segmented worm, with several segments already formed; the mouth is to the left. (3) The Nauplius larva of the goose-barnacle. (4 and 5) Two views of the Zoea larva of a crab. (6) The larva of Phoronis. (7) The larva of a sea-cucumber; its gut, with anus below, is seen by transparency. (8) The fully developed larva of the sand-worm Nereis; it has three segments with bristle-bearing swimming-organs or parapodia. (9) Young larva of a limpet. (10) Older limpet larva (veliger stage) with a shell and rudiment of a foot (to right). (11) The solid planula larva of Clytia, a hydroid polyp resembling Obelia. (12) The larva of a lampshell. (13) The same just after fixation and metamorphosis.

adaptations of floating life. In dinoflagellates, the projecting spines become more elongated in summer and in brackish water. Similarly, feathery hairs are only found in the copepods of warm seas, not in polar species. When one and the same species of plankton-animal is found in polar and tropical regions, it is often found that it lives at the surface in high latitudes, but in low latitudes floats deep, where not only temperature but viscosity is suitable. For the same reason, it would appear, floating animals inhabiting the same depth-stratum are smaller in warm than in cold water, for if they grew larger in warm seas they would sink deeper.

The same fact often brings about a depth-stratification of related forms according to size. For instance, the different species of the Radiolarian genus *Challengeria* get larger as we descend, apparently being mechanically sorted out by their ability to float, and the same is true of arrow-worms and certain prawns and fish. A good example is the Atlantic fish *Cyclothone microdon*. Its average length is about 1¼ inch at 500 metres depth, double as long at 1,500 metres.

This anti-sinking trick of increasing surface is, it will be noted, often combined with some power of swimming. If the swimmers wanted to get anywhere in particular, the friction of the extra surface would hinder them; but as their swimming is only meant to keep them up in the water, the spines and feathers save some expenditure of muscular or ciliary energy. The same is true for most of the other passive anti-sinking devices of pelagic life.

As protoplasm is a little heavier than sea-water, any dilution of living bodies with water will lighten them and make them sink more slowly; and if, as is usually the case, the water is bound within a jelly, this can help support the animals—it can act as a primitive skeleton.

Among the ranks of water-swollen jellified pelagic sea-beasts are the horde of jelly-fish, in some of which all but one per cent. of the body is water; all the comb-jellies and many siphonophores; swimming snails, and even octopuses and cuttle-fish; a few transparent fish; and the remarkable

leaf-like larvæ of the eels. In the pelagic sea-squirts, the Salps and Pyrosomes, the same result is achieved by having the tunic of cellulose swollen with water.

Other organisms do not merely dilute their weight but counteract it by accumulating lighter substances inside themselves. Sometimes, as in the common phosphorescent Noctiluca, the main flotation material may be merely water which is less salty and therefore lighter than sea-water. But in most cases, the much more efficient method of using fat or oil is adopted; the creature is buoyed up by the microscopic liquid balloons scattered through its tissues. For instance, most small pelagic Crustacea have abundant fat in their tissues, as does the pelagic clam, Planktomya. It is no accident that the food-reserves in the liver of Selachians and the abundant cod tribe are stored in the form of oil instead of the heavier glycogen of most vertebrates; it is interesting to reflect that, since vitamin A is soluble in oil or fat but not in other substances, the desirability of a low specific gravity has led to this vitamin, produced in abundance by the diatoms of the sea, being stored in easily accessible form in cod-liver oil, whereas had the specific gravity of the sea been a trifle greater, the cod might have stored its reserves as glycogen, and the bulk of the vitamin would have been destroyed in its body or excreted as waste.

Numerous free-floating fish-eggs, like those of mackerel, also owe their capacity of floating to oil-globules. The sunfishes (*Mola*) and gigantic basking sharks (*Cetorhinus*) lounge lazily at the surface; they are only enabled to do this by the thick layers of fat below their skin, which reduce their specific gravity to that of sea-water.

The layers of blubber found in whales, dolphins, seals, and penguins, though doubtless indispensable for the minimizing of heat-loss by their bad conduction, serve also a secondary purpose in lightening the animals, and so rendering more of their muscular energy available for directed activities.

The most efficient lightening mechanisms are balloons of air or other gas; but the construction of these involves a

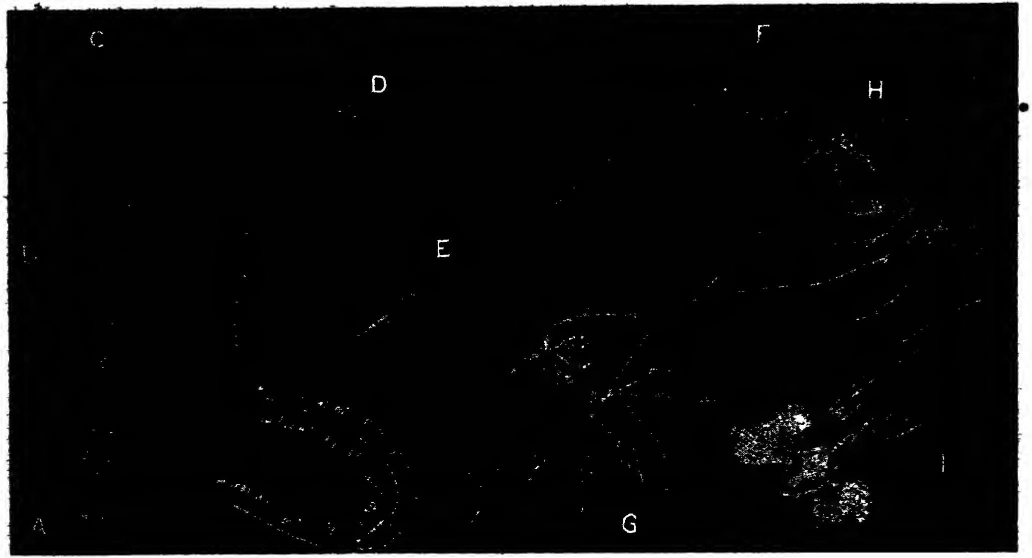

FIG. 5.—ADAPTATIONS TO A FLOATING LIFE.

(A) The phosphorescent protozoon Noctiluca is lightened by containing comparatively fresh water. The other organisms are (B) Glaucus, a sea-slug; (C) Calocalanus plumulosus, a copepod crustacean with a huge tail; (D and E) Two kinds of flagellate. (F) A chain of diatoms. (G) Another species of Calocalanus. (H) The larva of the rock-lobster or langouste, Palinurus. (I) The larva of the common angler-fish, Lophius. All these have spiny or feathery outgrowths to prevent sinking. In addition the last two have flattened anti-sinking planes.

Fig. 6.—Parallel Evolution towards the Bell-Shape in Creatures of the Open Sea.

Above is an octopus, Cirrothauma, which has become bell-like by growing a membrane between its arms. Below it are two individuals of the pink pelagic sea-cucumber, Pelagothuria, with a fringe of tentacles held together by webbing. The one on the left has just made a downward swimming stroke with its tentacles. Below on the right is a large jelly-fish, Stomolophus.

high degree of specialization, and they are not common. Many siphonophores have gas-glands which secrete gas into a special bladder; and the Pearly Nautilus and its strange relative Spirula still store gas in the chambers of their shells, as did all the Ammonites and Nautiloids of bygone eras. In one pelagic snail, Glaucus, the generation of gas by bacteria in the intestine has been turned to account, and the animal owes its capacity for floating to a flatulence made normal and physiological.

Gas-bladders are best developed in bony fish. The great majority of their abundant species owe their success to speed and directed activity; to secure this they must dispense with all such aids to flotation as jelly or protruding spines or flaps and concentrate on muscle and skeleton, and purity of stream-lined form. But as a result their tissues in general are a good deal heavier than sea-water, so that without a gas-bladder much of their energy would have to be expended in the never-ceasing task of fighting gravity. A few pelagic fish succeed in this task, such as the immensely powerful sharks. The common mackerel, too, like its close relative the tunny, has also lost its air-bladder, presumably to achieve greater speed; as the result of its unceasing activity during the feeding season, it has to recuperate for several months of the year resting on the bottom without eating.

Apart from such rare exceptions, active pelagic fish possess gas-bladders and are thereby enabled to regulate their specific gravity to that of the water in which they live, and so to utilize every ounce of their muscular power for pursuit or escape. If the gas-bladder had not been evolved, fish must have remained a predominantly shallow-water group because of the necessity of resting upon the bottom. As it is, the possession of a gas-bladder by almost all bony fish and the lack of it in all gristly fish like sharks and rays is reflected in the fact that a far greater proportion of the former are animals of the open water, while a far greater proportion of the latter spend most of their time near the bottom, alternately resting and indulging in sharp bursts of active swimming.

Gas-bladders may also act as sensitive pressure-recorders, the expansion or contraction of their contained gas telling the fish whether he is moving up to a region of less pressure or down to one of greater pressure. Terrestrial animals have no need of such pressure-sensitive indicators; and so when man invaded the three-dimensional world of the sea with his submarines, of the air with his aeroplanes, he had to devise pressure-gauges to act as artificial sense-organs for recording variations in vertical height.

Below a certain depth gas-bladders become very rare, owing to the physical difficulties of secreting gas against great pressure.

Finally, another method of reducing specific gravity is to cut down the skeleton as far as possible and to lighten its plan of construction. For instance, the one and only free-swimming sea-cucumber, Pelagothuria, is also the only member of its class to lack a protective mail of tiny, limy plates in the skin. The internal "bone" of pelagic cuttle-fishes is thin, horny, and limeless; and the pelagic bivalve mollusc Pelagomya has no lime in its shell; pelagic fish often have a much reduced skeleton, with a very low mineral content. The skeleton of crustacea shows a progressive diminution of mineral matter as we pass from permanent bottom-dwellers to permanently open-water forms. Free-swimming Copepods of the plankton only have six or seven per cent. of mineral matter in their constitution, and are lightened by having five or six per cent. of fat. The heavy crawling shore-crab, on the other hand, has less than three per cent. of fat, and over forty per cent. of mineral matter.

Before passing to the deep sea, mention must be made of the strange life of calm regions of the ocean, of which the Sargasso Sea is one of the largest and best known. The currents which flow past such calms abandon into them a proportion of the floating animals and plants which they are bearing along. In the Sargasso Sea the most important of such flotsam is the gulf-weed, *Sargassum bacciferum*. This grows on the coasts of the Caribbean Sea; pieces of it, broken off by the waves, float along in the Gulf Stream, supported

by their gas-bladders, and accumulate in dense masses in the calm zone. Eventually their bladders decay, and they sink and die without posterity. But meanwhile, before their death, they support an abundant crop of strange animals. Some of these exist elsewhere; but some live only in this curious accumulation of doomed plant fragments, constantly passing from one temporary home to another. The animals often resemble the weed in an extraordinary way, both in colour and form. The weed is golden-brown, patched white with colonies of Polyzoa and with little tube-living worms. This coloration is frequent among its inhabitants; and in addition they are often beset with fantastic ragged lappets and membranes which mimic the leaves and branches of the weed. These devices appear to have been developed as a protection against the attacks of the sharp-eyed sea-birds which hover above this seaweed garden of the calm.

§ 3

The Deep Sea

The inhabitants of the deep sea were to all intents and purposes unknown until the voyage of H.M.S. *Challenger* in 1872 to 1876. One of its objects was to discover the primitive ancestral forms of life which were suspected at that time to be lurking in the depths. This expectation, however, was unrealized. When the deep-sea creatures were eventually brought by human ingenuity to the light of day, they were often more grotesque and strange than any imagination had dared to picture, but they were not particularly primitive. All sorts of families of normal surface-living creatures, including some of the most modern and specialized groups, have in fact contributed immigrants to this strange region; and among fish almost all the deep-sea creatures belong to the less primitive group, the bony fish, very few to the more primitive sharks and rays.

No living Trilobites or sea-scorpions or extinct types of

Echinoderms, no Ammonites or Ostracoderms or primitive armoured fish have been hauled up to the light of an upper world that had outgrown them. It is possible that the marine abyss was such a difficult region to colonize that it stood largely untenanted through most of geological time, and that its invasion only began on a large scale when the more specialized types of sea-animals had come into existence—the prawns and crabs, the cuttle-fish and octopus, the bony fishes. Representatives of other groups had doubtless invaded it before, so that it was not as barren and empty as the land; but it offered no such encouragement and variety as the land, and so there was no blossoming of one or two special invading stocks into flourishing new groups, as happened with land plants or vertebrates or insects, but a sporadic fitting of a number of isolated types to the queer and specialized conditions, as has happened in other queer and specialized habitats like caves or salt lakes. Most authorities believe that the invasion of the great deeps by true fish began no earlier than Cretaceous times (IV C).

If all marine life depends on the plants which build themselves out of inorganic matter in the narrow illuminated zone, then obviously only this zone is biologically self-supporting, and the life at all greater depths must somehow exist at its expense. That is in fact so; deep-sea life is an unproductive assemblage of types nourished by scraps from the banquet spread above in the light of day.

Not every surface organism finds its fate in another's stomach. Thousands die from other causes, and their corpses, once their swimming movements cease, or their floats decay away, must sink towards the unilluminated depths. Over the whole of the ocean the rain of corpses proceeds without cessation, and the bottom is in large part covered with thick deposits made of their skeletons. This rain of death, however, gives life to all the deeper layers; for it is their only source of food. It is a constant stream of manna from above—often, it is true, in process of decomposition, but none the less nutritious.

The inhabitants of the regions passing down from the surface to the lightless abyss do not live haphazard at any depth. They each have their appointed place, each living out its life in its own particular layer of cold and silent blackness, often thousands of feet above the bottom, thousands of feet below the surface. The depth-range of some is comparatively large, while others are confined to a single level of the sea only a few hundred yards thick; and the zoning is complicated by the vertical movements which so many of the creatures nearer to the surface execute periodically every twenty-four hours, ascending at night and descending by day. None the less, the most striking feature of the life of the open sea is this stratification. Most pelagic animals live in definite storeys just as do the inhabitants of a skyscraping block of flats. We do not see the floors and roofs which limit the different zones. They are none the less perfectly real, and are constituted by the barriers set by degrees of temperature, pressure, and salinity, and by the kind of food available.

For the food-rain will, naturally, not be the same near the surface as it is in the depths. Each layer will contribute its quota of dead vegetation and corpses to the layers below; and each layer will take its toll of the corpses from the layers above, altering not only the quantity which finds its way farther downstairs, but also the quality, since not all kinds of corpses will be eaten in the same proportions. The total amount of the food-rain will grow progressively less, since at each level there is a wastage, due to bacterial decay, with consequent dissipation of solid food into unavailable solution. On the whole, the smaller particles, of which the tiny plants of the surface make a large proportion, will be snapped up or decay away before the larger, so that the average size of the drops of the food-rain will increase with depth. They will be the biggest particles, the quickest sinkers, and the less rapidly decaying lumps. They will be bigger and rarer. We should therefore expect to find, as we go downwards, first a decrease in the amount of life in general; then a

FIG. 7.—DEEP-SEA CREATURES: FOUR FISHES, TWO SQUIDS, AND A CRUSTACEAN.

Top left, Bathypterois, with degenerate eyes and long sensory feelers on its head. Top right, Pachystomias, predaceous, with a sensory whisker on its chin, and two luminous organs close to its huge eye. Upper centre, Chiasmodus, which is carrying a fish bigger than itself in its distensible stomach. Lower centre, Gastrostomus, with enormous gape; it also has a distensible belly. Lower, left and right, two squids, Toxeuma and Bathothauma, with huge stalked eyes. Below, centre, Eryoneicus, a blind prawn.

decrease in the proportion of current-feeding organisms, and an increase not only in carnivores, but especially in animals adapted for taking advantage of relatively large but infrequent mouthfuls. And these expectations are realized. The monstrous and fantastic deep-sea fish are all extraordinarily voracious, some with jaws capable of grasping and swallowing bodies larger than the normal size of the elastic devourer. Their lives are a prolonged fast, varied by some swift mouthful and repletion. The specimens of deep-sea animals obtained in nets have almost all been under a foot long, and it used to be supposed that the scarcity of food was so great that no larger creatures could exist in the depths. However, by the aid of the air-tight pressure-resisting chamber christened the bathysphere, invented by Otis Barton, Dr. Beebe has been able to venture down to more than half a mile below the ocean surface, and there, among many strange new forms of life, has seen large fish more than six feet long. We may conclude that only the small forms are likely to be taken in a net: these giants are too agile.

It is worth while anticipating our story a little, and reminding ourselves that essentially the same conditions hold in forests, especially evergreen forests, and most particularly in the tropical rain-forests. Here again light, coming from above, is life's prime mover. Seen from above, the forest has an exuberant surface of green dense leafage, inhabited by a thousand birds, mammals, and insects which never descend to the terrestrial depths. Below the bright surface is a dim twilight, with a much-diminished life, the plants consisting mainly of parasites sucking nourishment from the trunks of the trees, or vines and lianas climbing up them towards fuller light, or epiphytes seeding themselves on the great trees' leaves and branches; and the space from roof to floor is divided into definite zones of life. The floor of the forest, like that of the ocean, is covered with the debris of the upper layers. Leaf-corpses are continually floating down, twigs and fruits falling, with an occasional animal body. The most essential difference is that in the forest the food-rain

is not so slow-falling, and thus cannot be raided by layers of creatures on its way to the bottom. On the bottom it accumulates as mould, and gives nourishment to many fungi and bacteria and a horde of scavenging animals.

The tree-trunks support the illuminated surface. Competition between all the species and all the individuals of each species has finally resulted in a nearly flat sea of foliage, pushed heavenwards to the limit of the trunks' mechanical possibilities. The trunks are also supply-pipes, bringing the necessary nitrogen, sodium, chlorine and other mineral constituents of plant-protoplasm up from the soil to the life-factory of the leaves. There is nothing like this in the ocean; but even there, as we have seen in § 1 of this chapter, the depths provide essential mineral supplies to the plant-life of the surface. In any case, it is as well to be reminded of the fact that the forest, like the sea, has its productive region at its upper surface, and that the solid ground on which we men are compelled to walk through it is a dependent parasitic zone as truly as are the ocean depths.

The dependence upon a slow food-rain from above is the most important of the conditions influencing deep-sea life; and then, in order of descending importance, come the darkness, the cold, and the pressure. The pressure at great depths increases by almost exactly one atmosphere for every ten metres of water. At the bottom of the great deep near the Philippines (9,788 metres) the pressure would be over 960 times as great as the ordinary pressure of air at sea-level —equivalent to the weight of a column of mercury nearly half a mile high! No animals have yet been brought up from over 7,000 metres (about 23,000 feet), but this is probably due more to the enormous technical difficulties of dredging at greater depths than to an actual absence of animal life.

It used to be supposed a century ago that no animals could exist at depths over one or two thousand feet, owing to the pressure. As a matter of fact, these great pressures make singularly little difference to animals, for the simple reason

that the pressure of the water is externally the same on all sides, and is equalized internally by the pressure of the blood and the fluid contents of the cells. The animal exposed to a pressure equivalent to a quarter of a mile of mercury feels it no more than we feel the atmospheric pressure—15 pounds on every square inch of our bodies. The popular belief that the high pressure increases the density of the water so much that sunken ships would remain suspended when they reached a certain depth is quite unsound. Water is so incompressible that the increase in density at a depth of say 1,800 feet is only about 2½ per cent.; salt water with a specific gravity of 1·028 at the surface would at this depth have one of only 1·054.

Even the evil effects of rapidly bringing animals to the surface from the great pressures of the deeps have been much exaggerated. It is perfectly true that they are usually dead or dying when brought to the surface; but this is due much more to change of temperature than to change of pressure. This is shown by deep-sea hauls in the Mediterranean. The waters of this sea, owing to its excess evaporation, are more salty, and therefore heavier, than those of the Atlantic. Accordingly, the outflowing current in the Straits of Gibraltar sinks, and the inflowing current is near the surface. The Straits of Gibraltar make a sill nowhere more than 1,500 feet deep; and as a result only the highest and therefore the warmest layers of Atlantic water flow in. The Mediterranean thus receives no water colder than 12·9° C.; the whole of its contents from about 500 feet down to its greatest depths of nearly 13,000 feet are uniformly of this temperature. And we find that deep-sea animals can be brought to the surface in the Mediterranean, cuttle-fish for example, without showing any of the ill-effects which are suffered by kindred Atlantic animals brought up from the same depth.

The one exception to this innocuousness of pressure-change is afforded by fishes with closed gas-bladders. In spite of the arrangements which exist for resorbing gas from the bladder into solution in the blood, the expansion caused by

rapid decrease of pressure is too great, the bladder swells up enormously as the fish is hauled to the surface, and forces the entrails out at the mouth, or even blows the fish into fragments.

That rapid and considerable pressure-change need have no ill effect is shown by the large daily vertical migration of various creatures. Many plankton organisms and pelagic fish migrate up to near the surface by night and down to 400 or 500 metres by day. In spite of the forty-fold change of pressure to which they thus expose themselves twice in every twenty-four hours, they suffer no more than do Swiss goats and goatherds in their customary vertical wanderings, up by day and down to the villages at night.

Sperm-whales dive down to great depths in search of their prey, the giant cuttle-fish; and all whales do so when harpooned; they may traverse over 1,000 feet of vertical height in a minute or so, and some may be capable of diving to half a mile. A diver would die if he were hauled up from such depths so rapidly, through the appearance of bubbles of nitrogen in his blood (just as bubbles of carbonic acid gas appear in soda-water when it is released from the pressure within the siphon), which would then stop his circulation. Whales do not suffer in this way at all, largely, it would appear, through the presence of so-called *retia mirabilia* on their veins, " marvellous networks " where the vein breaks up into a great number of small vessels for a short section of its course. The gas-bubbles are probably caught in some of these small vessels and held there until they can be redissolved.

In all seas save the Mediterranean, temperature sinks steadily with depth. The average temperature for the great oceans is about 16° C. at 600 feet, only 10° at 1,200. At 3,000 it is only 4·5° C., while at 12,000 feet it is down again to 1·8° C.—only just above freezing. What is more, the deeper we go, the less variation is there in the temperature; at over 600 feet down, the seasonal change of temperature is trivial or nil. Nowhere else is life's environment, whether

as regards light, temperature, or chemical and physical conditions, so uniform as in the marine abyss.

The darkness in the depths is complete, save for what light is generated by their living inhabitants. Water rapidly cuts off light. Light pouring directly down penetrates much deeper than oblique light; thus beyond a certain depth only the noon-day sun will penetrate, and so the length of the day decreases with the depth. In the harbour of Funchal, Madeira, the 12-hour March day is reduced to 5 hours at 30 metres depth, to a mere 15 minutes at 40 metres. Beebe in his bathysphere sometimes saw traces of light at over 500 metres, but this is exceptional. In general, light sufficient for the needs of green plants extends down only to about 100 metres. The great majority of marine plants live in the first 50 metres; at 75 metres there are only half as many plant individuals as at 50 metres. Below about 200 metres, the only plants which exist are sinking downwards dead or damaged. Below this, the deep sea begins, with no living green plants and no true vegetarian animals, but only decay-producers, scavengers, and predatory creatures.

The longer wavelengths of light are more quickly absorbed by water than are the shorter. All the red rays are absorbed soon after 100 metres, and all the green before 500, but a trace of violet penetrates deeper than 1,000 metres. Even at 30 metres, a diver cannot see red objects as red; there is no red light for them to reflect and so they look black, while from here on the surroundings are brilliant blue.

Most animals from the illuminated surface zone are of crystal transparency (sometimes, however, with a few internal organs which cannot be rendered transparent, gathered into a dark knot which simulates a fragment of floating weed). When colour is present, it is generally blue, as in the Portuguese Man-o'-war and other siphonophores, some Copepods, and the lovely floating snail Ianthina. Many surface fish are bluish or greenish above, silvery below, like the mackerel. These colours, like transparency, would appear to have

some protective value in the blue sea-water, though transparency seems to take its origin as a mere accident of jellification.

But in the depths, to reflect no light and so to fade into the surrounding blackness is the best means of protection from all those enemies which hunt by sight. And as red then looks black, red shares predominance with black and other dark colours such as deep brown or purple-black. Some groups, such as the fish, seem to find it difficult to produce red pigment, and in the deep sea incline to black; other deep-sea groups, such as Crustacea, are almost without exception red. There are also red Foraminifera and polyps, red sea-anemones and starfish, red octopuses and cuttle-fish, and even red arrow-worms. An interesting case is Velella, one of the siphonophores. This, when adult, floats at the surface, with a sail projecting up into the air, and both animal and sail are a lovely blue. Its larva, however, lives in the deep sea and is red; it only becomes blue when it ascends to adult life at the surface.

Although some deep-sea gelatinous animals retain their crystalline appearance, yet jelly need not necessarily involve transparency, as is shown by the fact that many deep-sea jelly-fish and arrow-worms are dark-coloured or red; some, such as the jelly-fish Atolla, have their surface representatives transparent, and grow darker and darker with depth.

At the depths where these red prawns and black fishes live, whatever light is visible is produced by the animals themselves. Phosphorescent organs occur in almost every group of deep-sea animals, both bottom-living and pelagic, in polyps and corals, starfish and bristle-worms, cuttle-fish, crustacea and fish. These organs are of various kinds. Most of the fixed bottom-living forms—sea-pens, sea-fans, and so forth—shine all over, diffusely, often with a marvellous radiance. It may be that phosphorescence of this type is a mere accident, serving no useful purpose, and that for unknown reasons conditions in the deep sea are especially favourable to its production. There are phosphorescent

animals in plenty at the surface of the sea, and the luminosity of some of them, such as the abundant Noctiluca, seems to be as functionless and accidental as that of fungi on rotten wood. On the other hand, animals of this diffusely phosphorescent type are more abundant and produce more brilliant light in the deep sea than elsewhere. It has been suggested that the light serves to lure small fish and other prey within range of the polyps and their paralysing tentacles.

This is made more probable by the extraordinary luminous organs of deep-sea angler-fish, which undoubtedly act as lures for prey. The shallow-water angler (Lophius) lies flat and well concealed on the bottom, with its huge predaceous mouth facing upwards. It grows a fishing-rod and bait on its head. The foremost ray of its dorsal fin has suffered a curious transformation; it is elongated, detached from the rest of its fins, and bears at its end an enlarged flap of membrane. The jerking of this attracts inquisitive and hungry fishlets, which in a moment are snapped up by the unsuspected jaws just below. As Aristotle observed more than 2,000 years ago: "They are often caught with mullet, the swiftest of fish, in their interior. Furthermore, the frog-fish is usually thin when he is caught after losing the tips of his filaments." In the deep sea, numerous members of this same family are found (though they are all much smaller in size); they also all attract their prey by means of lures, but these lures are always luminous. Perhaps the most extraordinary of these animals is Lasiognathus, whose fishing-rod, in addition to possessing a luminous lure, has a hinge in the middle and hooks at the tip. It seems to be thrown forwards when prey has been attracted near by the light, and then jerked back so as to impale them on the hooks.

It is as recognition-marks that the luminous organs of deep-sea animals have their most frequent significance. The prowling population can never be dense; and without special advertisement it would often be difficult for the sexes to find each other. The advertisement takes the form of a pattern of luminous organs, each species having its own characteristic

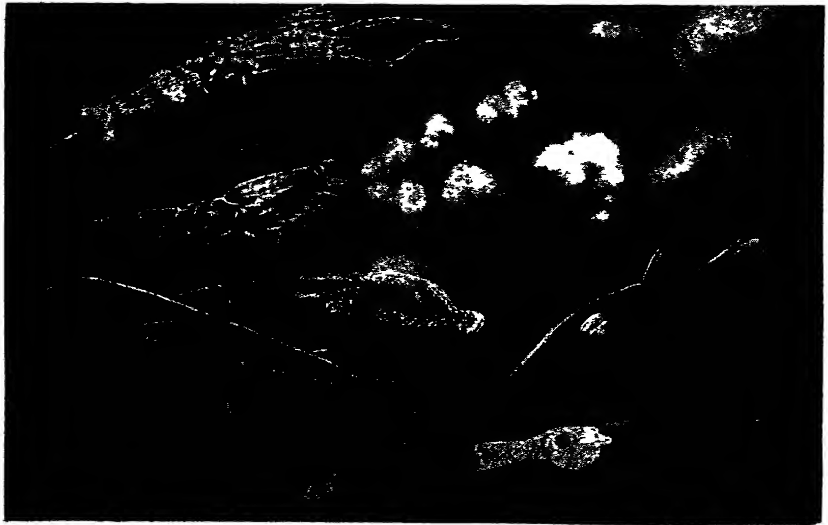

FIG. 8.—LUMINOSITY IN THE DEEP SEA.

Top left, the squid Pterygoteuthis, with big eyes and a pattern of luminous organs on head and trunk. Below it, the prawn Heterocarpus puffing out clouds of luminous secretion to baffle its pursuers. Centre, the gastropod mollusc Phyllirrhöe, with many small light-organs. Below, three fishes: from left to right, Vinciguerria, with light-organs looking like illuminated portholes; Gigantactis, with a luminous nose which serves as a lure; and Aulastomatomorpha, with its whole face and head luminous.

arrangement. Sometimes there is a single row of small lights down the body; sometimes tiers of lights, so that the fish looks like a liner at night; deep-sea cuttle-fish generally have a pattern dotted over their body and arms; some animals, both fish and cuttle-fish, make play with lights of different colours, or with different-sized lights. In any case, each species thus carries its own identity written upon it in letters of cold fire, can know its own kind at a distance, can recognize such or such a pattern as the badge of its enemy, this other as the badge of its prey.

But there are other uses of luminosity. Shallow-water cuttle-fish escape from their enemies under cover of a smoke-screen of ejected ink. This would be of no service where all is already black; and accordingly we find that some of their deep-sea relatives squirt out a luminous cloud to confuse pursuers. The same trick is played by certain deep-sea prawns.

Finally there are the luminous organs designed, like head-lights, to facilitate the animal's own seeing. The most curious example of this is the living torch carried by a hermit-crab from the Indian Ocean. Like many other kinds of hermit-crab, this animal carries on its snail-shell house a sea-anemone as partner. Doubtless the sea-anemone profits as do its fellows in similar situations in shallow water, by catching crumbs that fall from the crab's table. The benefit conferred in return is normally that of protection, by means of the serried batteries of stinging cells on the anemone's tentacles and the formidable stinging threads, which it can protrude through the portholes in the wall of its body or through its mouth. But in this case the anemone is phosphorescent, and confers the boon of light as well.

Frequently, in deep-sea fish, cuttle-fish, and crustacea alike, there is a concentration of especially large light-organs near the eye, and in some cases these have evolved into veritable projectors. Cells which generate a luminous secretion are placed in front of a curved reflector made of a glistening membrane backed by black pigment, and the

outward-streaming light is concentrated into a beam by means of a lens.

Where light is so scarce and so dim, eyes may be expected to evolve in one or other of two opposite directions. Either they may degenerate, wholly or in part, and the animal make up for its lack of vision by an excess development of other senses such as touch; or else they may be enlarged and improved to the pitch of extreme sensibility so as to catch every faint glimmer of light. Both of these methods are found in deep-sea animals. On the whole, the balance has been in favour of keeping and improving the eye. But bottom-livers leading a crawling-feeding life show eye-degeneration more frequently than do open-water creatures, and in both situations the more active kinds of creatures tend to enlarge their eyes, the less active to lose them.

In general, those deep-sea animals which have well-developed eyes include those which have definite arrangements of luminous organs, and, of course, those which possess searchlight organs. Recognition-marks would be useless to a blind animal. But the deep-sea anglers are often themselves blind. Their light is aimed at other species; and so long as the inquisitive prey is lured alongside, it does not matter whether sight, touch, or any other sense is used to detect its presence.

Sometimes the eyes are positively enormous; in the crustacean Cystisoma the eye occupies at least two-thirds of the surface of the head. In other deep-sea creatures (and nowhere else in nature), the so-called "telescopic eye" is found, which has been independently developed in eight sub-orders of deep-sea fish and in one cuttle-fish, while a somewhat similar arrangement is found in some deep-sea crustacea. This type of eye, to be precise, is not "telescopic" at all, it is an adaptation to save space. The bigger the surface of the lens, the more light does it collect, the more it approaches the spherical in shape, the more does it concentrate the light that falls upon its surface. With a lens as large as exists in many telescopic-eyed fish, an eye of the

usual spherical type would be as big as the whole head. The so-called telescopic eye is simply the central cylindrical portion of an eye, with a spherical lens. All the light that falls on it is concentrated upon a very small patch of retina, and range of vision is sacrificed to the pressing need for light-collection and concentration (Fig. 9).

Even with such eyes, sight in the deep sea may well need to be supplemented; and accordingly it is common to find extraordinary developments of touch-organs, such as barbels, often long and strangely branched, on the head or throat, or elongated spines or fin-rays acting like cat's whiskers, and most deep-sea fish have the mysterious lateral-line sense-organs better developed than their surface relatives.

One unique result of deep-sea life is the development of parasitism in the males of certain angler-fish. In these species, until recently, only females were known. Eventually some of these females were discovered to have growing on their bodies strange objects not unlike miniature and deformed fish. Further investigation showed these to be indeed fish—the long looked-for males of the species. When quite young they apparently bite on to the female, gradually embedding their snout in her skin. Both skin and blood-vessels of male and female grow together, and the male becomes a true parasite, nourished entirely at the female's expense. His heart and digestive system degenerate, and the bulk of his body becomes filled with testis. Presumably when the female lays her eggs, some chemical stimulus acts upon the male and causes him to eject his fertilizing sperm at the same time.

The difficulty of male and female finding each other at mating-time in the dark and sparsely populated waters of the deep pelagic zone must be very great. This strange state of affairs—the only case of thorough-going parasitism in vertebrates—is without doubt a method for circumventing this difficulty.

§ 4

On the Floor of the Abyss

Near inshore the bottom of the sea is covered with deposits derived from the land, eroded bits of land carried out to sea by rivers. Naturally the heavier particles settle first, so that in general the farther from the land, the finer-grained are the deposits. Such land-derived deposits, however, are rare at depths of over 600 feet. Below that depth the floor of the ocean is covered with layers of material derived either from the skeletons of the animals and plants that live above, in the upper storeys of the sea, or else from volcanic dust. Some of the organic materials are predominantly limy, such as globigerina ooze largely made of the skeletons of that little foraminiferan, or the much rarer pteropod ooze in which the shells of those active swimming mollusca predominate. Others are mainly flinty, such as diatom ooze and radiolarian ooze. The finely powdered volcanic accumulations are known as red clay.

The calcareous deposits are poor or absent in high latitudes, owing to the difficulty of secreting a calcareous skeleton at low temperatures. They also never occur below a certain depth, usually about 15,000 feet, since under great pressures the calcareous matter passes into solution. But they have an enormous extent: globigerina ooze, especially abundant in the North Atlantic, covers nearly thirty per cent. of the whole ocean bottom. Siliceous deposits can go a little deeper without being dissolved. They are especially abundant in colder seas, and in regions where the water contains much siliceous matter, for instance in many parts of the Indian Ocean, but cover less than ten per cent. of the ocean bottom. Finally, in increasing quantities from a depth of 13,000 feet downwards, comes the red clay, covering over a third of the whole sea-bed. Only over very small areas is the ocean floor clear of ooze—here and there where deep currents flow powerfully, perhaps here and there

FIG. 9.—"TELESCOPE EYES" AND OTHER ADAPTATIONS FOR SEEING IN DIM LIGHT.

Above, the cephalopod Amphitritus. Centre, two fish: upper, Gigantura; lower, Argyropelecus. Below, two views of the crustacean Cystisoma, with eyes so big that they cover all the upper surface of the head and meet on the crown like a dragon-fly's. The eyes of Gigantura look forwards; all the others look upwards.

where a rare slope occurs steep enough to shed its accumulations.

All these deposits have two things in common—they are soft, with a consistency something like that of butter on a very hot day; and they contain all the debris of the food-rain which has escaped the population above.

It pays many organisms to sift and scavenge in and on and close above this rich ooze; but precaution must be taken by the surface animals not to sink in, and by the pure current-producers not to have their works clogged with the fine ooze. The surface scavengers and predaceous animals almost all show devices for spreading their weight over a large area. Some of the spider-crabs and other crustacea have enormously developed legs, often with bristles or feather-hairs at the tips; some of the flat, cake-like sea-urchins of the deep sea have an expanded disk-like surface, and the sea-cucumbers have a special flattened sole. One or two of the current-producers have similar devices, such as the sponges which possess projecting collars of long spicules to prevent them sinking in the mud. But the great majority are stalked. Stalked sponges, stalked sea-lilies, stalked corals, stalked single polyps, stalked polyp colonies like the sea-pens with their strange bulb-like base thrust into the slime for anchorage, even stalked lampshells, sit balanced above the suffocating mud, on whose surface precariously crawl and forage the tribes of active scavengers (Fig. 10).

The Hexactinellids or glass-sponges are almost entirely confined to the deep sea. They differ from all other sponges in the open lattice-work of their construction. The best known Hexactinellid is the lovely Venus's Flower-basket from the deeps off Japan. We marvel at its delicacy and beauty; but we generally fail to ask ourselves the biological reason for the construction which confers such properties. A simple reason, however, does exist. Since warm water has a lower specific gravity than cold, any currents flowing polewards from the warmed surface of tropical seas will, like the Gulf Stream, float upon the top; and the necessary

return flow of chilled water from the poles will flow along the bottom. The Hexactinellids grow in the path of these

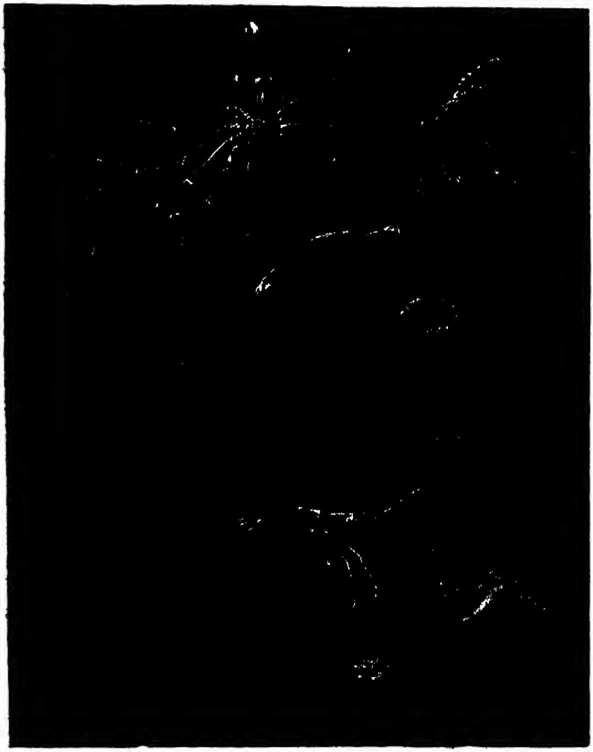

FIG. 10.—LIFE ON THE MUDDY FLOOR OF THE DEEP SEA.

Sea-squirts (left) and glass-sponges (right) are carried clear of the mud on long stalks. Sea-anemones grow on the sea-squirts, and Pycnogonids crawl over them. A prawn walks over the mud on enormous stilt-like legs, and flattened sea-woodlice and starfish crawl on its soft surface. *(Based on an exhibit in the Natural History Museum, London, of animals collected by the "Discovery" Expedition.)*

slow but constant bottom-currents. They can afford to dispense with all the current-producing machinery of the

ordinary sponge, and can simply spread a lattice-net in the path of the debris-laden stream.

As Dr. Bidder writes of the group as a whole:

> Food is brought to them, waste is taken away. For them in their eternal abyss, with its time-like stream, there is no hurry, there is no return. Such an organism becomes a mere living screen between the used half of the universe and the unused half—a moment of active metabolism between the unknown future and the exhausted past.

§ 5

Seashore Life

And now let us return from the extreme specialization of the deep sea to the primitive cradle of life—the shore, the intertidal region. It is so familiar to most people, and has been well described in so many admirable books, from Charles Kingsley's *Glaucus* to Flatteley and Walton's *Biology of the Sea-shore*, that we, with space pressing, can afford to treat it briefly.

We can best define the seashore as the strip of earth's surface between the highest land wetted by the sea in storms and the lowest low-tide mark. It has a very great biological interest. It is a zone of sharp transition from dry-land to salt-water; and, though a zone of transition, it is a permanent feature of our world. The outlines of sea and land may shift over the globe; but there is always a shore. Twice a day most of it is covered by water, and twice a day uncovered to the air as the tide ebbs off it. Thus, of all the habitats in the world, the shore is exposed to the greatest fluctuations and has the most variable conditions of life, in the completest contrast with the seasonless, dayless, changeless depths.

As we step across the shore from high-water mark to bathe at low tide, each point that we cross is exposed to a longer daily dose of water, a shorter dose of air. Accordingly, the shore is split up into parallel belts or zones of life according to the capacity of its animals and plants to resist exposure

to air. At extreme high-water mark, or even above it, flicked only by occasional spray, there are still barnacles and the dwarf species of periwinkle, there are green seaweeds in the brackish pools, and the sea-slater Ligia runs about among the stones, a giant woodlouse that is tied here between sea and land. Between tide-marks brown seaweeds predominate, a number of kinds of them zone by zone as we descend. Most have gas-bladders on their leaves to lift them up towards the light directly the waters cover them, and to help minimize the danger of being smashed against the rocks by breakers.

Below them comes a zone of great ribbon-weeds (Laminaria), that are only uncovered at the lowest spring tides; and these are mixed with many red seaweeds, which grow rapidly scarcer as we return landwards.

The creatures of the shore wake to activity not once but twice in every twenty-four hours, when the tide comes up and they can expand in the salt embrace of sea-water, the primeval fluid that bathes and supports, brings food and distributes marrying cells and spores. Many of the obvious characteristics of seashore creatures are devices for living through the periods between the vivifying visits of the water. The barnacle has its doors uncompromisingly shut while it is in air. The door, however, is on the chain rather than barred and bolted tight. The slight sizzling noise you may hear on a still day on barnacle-encrusted rocks is the multitudinous tiny bubbling of the thousands of fixed and shell-imprisoned crustaceans. Then, for an hour or so each day, when the waters solicit attention, the panels slide back and the microscopic casting-net of feathered legs begins its rhythmic task. The limpet, under water, makes journeys a few yards long, to browse on weed; when the tide falls he returns to his familiar home, a slight depression in the rock which he has worn, and sits upon it with tent-like shell just raised to admit air. The mussels, as the tide goes out, change from busy sifters of debris to passive lumps of flesh shut in a strong blue shell. Tube-worms when under the unsubstantial air are all deep in their tubes, waiting for the

water's renewal before they spread their flower-like tentacles; many of them have little doors to close the mouths of their homes.

The flattened shape of shore-crabs is adapted for retreat into crevices when the tide goes down; there to stay, audibly bubbling as they breathe, until the water rises again and they can sally forth on their scavenging jobs. In the moist miniature caves under rock ledges, sea-squirts and brilliantly coloured soft crusts of sponge wait with their apertures tight closed; sea-anemones are converted from carnivorous flowers to mere jelly-blobs. Some sponges that live in this situation differ from their permanently submerged relatives, which are barrel-shaped, in being flat and leaf-like: when the tide ebbs away, their two sides come together and retain a film of water.

Out on the sand and the mud, life disappears when the tide goes down. The buried cockles and clams and razor-shells withdraw their siphons—water-inlets and outlets—far beneath the surface, and the sand-eels burrow deep. Many creatures seek refuge from the air under stones—crabs and other small crustaceans of many kinds, little starfish, long green or black nemertine worms coiled up like skeins of ribbon. Even some fish and an occasional young conger can be uncovered by turning over the rocks between tide-marks. Among the colonies of hydroids and polyzoa that grow on rock and weed the tiny polyps are all withdrawn into their sheltering cups, which are often provided with some form of lid; and the periwinkles, withdrawn into their strong shells, close their homes with the horny door they carry attached to their foot.

But hard upon the retreat of the waters comes another fauna—a multitude of birds and mammals (man the chief among the latter) searching the pools and sounding the mud for the hiding water-feeders. Here and there in this world of waiting, hidden creatures are pools left by the retreating sea; and in these the varied population is a revelation to the ordinary landsman. There are so many patterns of life

among them which he has never met before, so many unfamiliar ways of living. The rock-pools are seas in miniature. There you may find animals getting their food by ways unknown on land—current-sifting tube-worms and molluscs, plant-like tentacle-spreaders like hydroids and sea-anemones (it is an unforgettable sight to see an unwary fish, venturing too near one of these animal blossoms, suddenly trapped and paralysed by a tentacle and drawn down to the gaping mouth); animals which browse, not on plants, but on other animals, like the lovely eolid sea-slugs that nibble hydroid polyps (and store up the nettle-cells of their prey, unexploded, in the tentacle-like projections, full of outgrowths of liver, with which their upper surface is beset, thus arming themselves with borrowed weapons). There, too, you may see animals which still reproduce by discharging a whole population of cells into the ambient water; animals with no head, like starfish; and animals with no mouth, like sponges. To watch and cogitate upon the life of a rock-pool near low-tide mark is to take a broad elementary course in marine biology.

There are three main types of shore habitat—rocky, sandy, muddy. On rock, sea-life is adapted for clinging tight, for resisting the pounding of the waves, for retreating into cracks. Hence limpets, barnacles, dog-whelks, tough brown seaweeds, flattened crabby creatures, encrusting sponges and sea-squirts. On sand and mud the urge is to burrowing. At this game worms and clams are supreme, but there are also heart-urchins and a certain number of crustaceans, and even one or two peculiar sea-anemones. The animals often have remarkable anti-clogging adaptations, so that they can breathe in spite of sand and mud all round them. The crab Calappa has its claws converted into tight-fitting doors that keep out sand, leaving only two pairs of holes in front for the entrance and exit of the vital respiratory current. And others, such as Corystes or Albunea, conduct clean water down to their gills through a " siphon " made of their two antennæ joined to form a tube by the hairs along their edges.

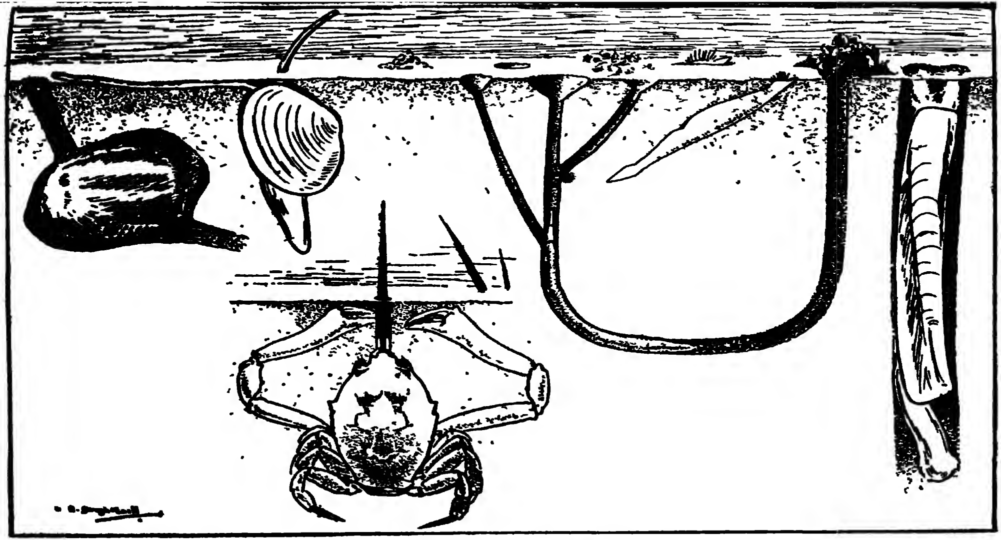

FIG. 11.—ADAPTATION TO LIFE IN SAND.

From left to right: A heart-urchin eating sand in its burrow; it keeps the entrance passage open by means of a special long tube-foot. A clam with its inlet-tube collecting water and fine particles from the surface of the sand, its outlet-tube discharging upwards. A tube of Balanoglossus. The tube is about eighteen inches deep; the sand which the animal eats is pushed out as castings. Between the inlet and outlet is an Amphioxus with only its mouth protruding; another mouth is seen farther away. A razor-shell clam with inlet and outlet tubes above and the distensible foot with which it burrows protruded below. Inset below, the crab Corystes breathing by a tube formed by its antennæ.

On some tidal mud-flats the eel-grass can grow—one of the very few flowering plants that have re-invaded sea-water, and so one of the very rare sea-plants with true, absorptive roots—and its long ribbons provide a habitat in themselves for animals. There we find pipe-fish (swimming and resting upright, to simulate the grass fronds); the queer crustacean Squilla with its claws built to close into a groove like the blade of a knife; cœlenterates like Haliclystus attached to the leaves; and many sea-snails.

Below the range of the tides, the inhabitants of sand, mud, or rock continue to show the same general differences as between tide-marks. Creatures with special adaptations for temporary exposure to air are, of course, no longer found; but a greater abundance of fully marine animals takes their place. The number of free-moving animals especially increases below tide-marks, notably the fish and crustaceans. On rocky ground the fish tend to resemble their surroundings protectively by their blotchy colouring and projecting tags of skin that break their outline; the swimming crustaceans, such as prawns, are a transparent green. On sandy bottoms the most typical crustacean is the shrimp. Shrimps, like flat-fish, are strikingly protective in their colour, and both types have the instinct to burrow down and lie half-buried in the sand.

The abundance of life in this well-lit zone beyond low-tide mark is extraordinary. This bottom-supply is of the greatest importance to many kinds of fisheries. Plaice, for instance, are bottom-feeders, much the most important item on their menu (in the North Sea, at least) being a little clam called Spisula. Spisula is exceptionally abundant on the Dogger Bank, and this is why the Dogger is such good fishing ground. Indeed, experiments with marked fish show that on the Dogger Bank plaice grow almost twice as fast as off the Dutch coast.

Between tide-marks, the zones of life are dependent upon times in and out of water. Below the reach of the tides, zoning of this sort disappears, and its place is taken by a

zoning dependent on the rapidly decreasing light-intensity. But this we have already discussed (§ 3).

§ 6

Coral Reefs and Islands

No account of the world's habitats would be complete without some mention of corals and their work. The formation of whole islands for the habitation of man by the unceasing industry of the tiny polyps (or "coral-insects," as they are still sometimes called in popular books—a survival from certain pre-Linnæan attempts at zoological classification !) has always fascinated the human imagination; and the sheer beauty, the strangeness and the variety of a coral reef have captivated all lucky enough to set their eyes on one.

Corals, broadly speaking, are polyps, belonging to the cœlenterate phylum, which secrete a skeleton, in most cases of lime. Most of them, but by no means all, belong to the same group as the sea-anemones. Like sea-anemones, they consist, roughly speaking, of an animated stomach with a mouth at one end, round which a circle of tentacles, richly set with stinging-cells, spreads ready to catch and paralyse living victims, and stuff them into the cavity within. Most of them, too, are colonial, but there are plenty of solitary "cup-corals." The variety of their growth and construction is very great. Some, like the organ-pipe coral, grow as parallel tubes; others are branching and tree-like, like the precious coral or the stags-horn; others again, like the brain-corals, produce great rounded masses of limestone; still others grow into flat, ridged disks, which look like the top of a mushroom turned upside down and converted into stone.

There are two very important facts about coral biology which help us to understand how reefs are made. The first is that corals afford an instance of biological partnership, or symbiosis—a phenomenon discussed more fully in Chapter IV (p. 131). Most species of corals contain, within their own

cells, great numbers of minute green plants. These plants, although they live in swarms in the tissues of the corals, are apparently not parasites but partners of their hosts. By consuming the abundant nitrogenous waste-products of the carnivorous coral's life-processes, they assist its excretion. It used to be supposed that they helped by serving as a food-source and being digested when the coral is short of its normal prey, but recent investigation has disproved this. But, however they do it, the plants are essential to their possessors; without their aid the polyps cannot flourish. And accordingly all such types are restricted to shallow water, where enough light penetrates for the green plants to utilize their energy-trapping powers. Reef-building corals are scarcely ever found below twenty-five fathoms.

The other point is one of more general application. It is that, for chemical reasons into which we need not enter, animals find it much harder to extract calcium from cold than from warm sea-water. And since calcium is the main ingredient of limy skeletons, animals with such skeletons flourish much better in warm seas. In almost all groups the number of kinds of animals that scaffold themselves with lime decreases rather rapidly as we pass polewards, and in polar seas the horny substance chitin largely replaces lime as the chief material for skeletons. Corals are one of the best instances of this rule. There do exist solitary corals in north temperate waters, but reef-building corals will not grow where the temperature of the surface water falls below 70° F.

These two peculiarities restrict coral reefs to the shallow water of an equatorial girdle rather broader than the tropics. And this has, as further consequence, that, of all the calcium dissolved out of limestone rocks and poured into the sea by rivers, a great mass is being built up in solid form in this girdle which the world wears round its middle, and very little anywhere else.

Three chief kinds of coral reefs exist. There are fringing reefs which hug the coast and have no deep-water channel between them and the land. Then there are barrier reefs,

which enclose a lagoon, usually deep enough for ships, but never over fifty fathoms, between themselves and the coast; and finally there are atolls, which do not border land at all, but consist merely of a coral platform rising out of the sea, its central cup covered with water and forming a lagoon, its rim raised to make a more or less continuous above-water circle.

Fringing reefs one can easily understand; they are what we should expect to find where conditions off a coast allow the growth of corals. But how explain the barrier reef and the atoll, with their wide lagoons and their steep outer slope, often extending down hundreds of fathoms into deep water? How can the deep foundations of these dams and pyramids have been laid, if the polyps cannot live more than a few fathoms below the surface?

Darwin sought to explain their origin by supposing a subsidence of land fringed by such a reef. As the land sank, new coral growth would be built up on the old. The reef would grow in height, and it would extend inwards as the land area shrank. Blocks of coral, piled up by the waves and cemented together by lime, would make a rampart on its seaward side, while the scour of currents in some places and the deposits of fine mud and sand in others would check the coral growth within this raised edge, thus giving us both barrier and lagoon. If submergence were continued until the last vestige of the original land had disappeared beneath the water level, the barrier reef would be converted into an atoll.

This theory, while it undoubtedly accounts for some of the facts, will by no means explain them all. It has since been pointed out that atolls might come into being in other ways. Submarine eruptions are not infrequent, geologically speaking, and may throw up volcanic cones above sea-level; but the erosive action of the waves is so great that such piles of debris, unless very large, are quickly eaten away and their tops eventually smoothed off flat well below the surface, thus providing an ideal platform for a future atoll. Indeed,

wherever land is rising, but rising slowly enough for the waves to plane its head or its shoulders down to such a platform, atolls or barrier reefs may grow.

Still another view suggests that, however originated, the coral reefs that we know to-day have made most of their growth since the Ice Age. For during the main glaciations so much water was locked up on land in the ice-sheets that the sea's level was considerably lowered; and when this solid water was melted and restored to the sea the resulting submergence would mean rapid upward growth of corals. In support of this we have the calculations of Dr. Mayer, who showed that for Samoa, at the present rate of growth, all the existing reefs could have been formed since the Ice Age. And from other regions comes evidence of the decay rather than the growth of reefs, as if the rapid growth favoured by the post-glacial submergence was now choking itself.

But whatever be the origin of coral lagoons, there is no doubt that they provide a peculiar, varied and very lovely habitat. Mr. Beebe, in his *Beneath Tropic Seas*, has described the beauties of this submarine world as seen from a diving-dress; and Mr. Pritchard has even sat under water in a diving-dress to paint them for us in colours and media that are unaffected by sea-water. The coral pillars shoot up from the floor of coral sand over coral rock; there are arches, doorways, caverns of coral. Fish of fantastic brilliance dart in and out, the crevices are full of strange worms and crabs, here and there the lagoon floor is scattered with star-fish and sea-urchins and bright-coloured shells. And the lives of all these creatures are centred upon the dominant growths of coral, these strange compounds of flower-like polyp and microscopic green vegetables, as the lives of all the animals and plants of a tropical forest are centred upon the trees, or the lives of all the prairie fauna upon grass.

§ 7

Holes and Corners of Sea-life

One could continue telling of sea-life through all this volume and never be done, so rich and various it is. But we have the life of the land before us still, and we must be brief. In this last marine section we will bring together some of the sea's interesting minor habitats. One of the most remarkable of special seashore habitats is the mangrove swamp, found so often in estuaries and along flat muddy shore in the tropics. Here the strangest mixture of creatures from land, fresh-water and sea meet each other. The mangroves and other kinds of trees invade the mud-flats, using their roots as stilts to keep their stems high. Millions of crabs dodge in and out of the roots; the mud is often as full of holes as a sieve—the work of armies of fiddler-crabs, the males with brilliantly coloured claws as big as their bodies, who scurry over the surface and pop sideways in and out of the holes; oysters grow on the mangrove-roots; the half-terrestrial fish Periopthalmus skips over the mud with the aid of its fins; at low tide the ants, descending from their nests in the trees, may be seen as they forage over the mud round pools in which sea-anemones still spread their tentacles; and birds, lizards, and monkeys come down to steal what they can from the sea's harvest.

The mangroves live by turning their roots into stilts; and they reproduce themselves by making dibbles of their seedlings. An ordinary seed or fruit simply dropped on to the mud would be washed away by the tide. Accordingly, the mangrove fruit is never shed, and the young plant actually germinates within it. In the course of six or eight months it develops a long, solid spike-like outgrowth, a foot or eighteen inches long and up to an inch or more thick, which forces its way out through the fruit-wall. At last the whole embryo plant, now weighing about three ounces, breaks loose from its parent, and falls, heavy and spear-like,

Thus it stabs itself into the mud, penetrating thither even at high tide through a foot or so of water. And at once it expands its leaves and begins to grow.

A widely distributed way of under-sea life is that of the boring animals, some tunnelling in wood, some in the shells of other creatures, some even in solid stone. The wood-borers are still the cause of great damage to wharfs and piers, and the worst of them, the much-dreaded shipworm, was in the days of wooden hulls the cause of serious loss among ships. Drake's *Golden Hind* was infested with shipworms; and at one time their burrowings in the timbers of Dutch dykes threatened to let the sea in over Holland.

The shipworm, Teredo, is a bivalve mollusc, whose body has been elongated till it looks much less like a mollusc than a worm, while its shell is reduced to a pair of hard chisels at one end, which are moved up and down by powerful muscles and serve to excavate the animal's burrow in the wood. The shipworm is further remarkable in that it is one of the few highly organized animals capable of digesting wood-fibre. Its stomach secretes a digestive ferment which converts some of the wood into sugars. It is the only boring animal in the sea which is entirely dependent for food as well as for shelter on the material in which it bores; and it is so strangely specialized that it can only begin a burrow at one very early stage of its existence. If an adult shipworm is taken out of its burrow, it cannot make a new one, but dies helplessly. British shipworms are rarely more than eighteen inches long, but there is a tropical giant which may grow as thick as a man's arm, and six feet in length.

Crustacea as well as molluscs take to wood-boring; among them the gribble (*Limnoria*) is the worst offender. These are tiny creatures, related to the wood-lice, which rasp themselves tunnels with their jaws. Usually they live by pairs, a male and a female in each burrow, the female apparently doing most of the work. The damage they can do may be realized from the fact that up to four hundred of them have been found under one square inch of wood surface.

Among shell-borers the sponge Cliona is the best known. Its boring activities (carried out apparently by chemical means) are the cause of the holes and tunnellings so frequently seen in oyster shells. It burrows also into limestone. This sponge is the cause of considerable loss on some oyster-beds, for when it is really flourishing it may kill oysters by completely rotting and disintegrating their shells.

Another borer which uses chemicals is the date-mussel of warm seas; it burrows into limestone by dissolving it with acid from a special gland. The familiar piddock or Pholas, however, rasps holes in rocks of various kinds by means of its shell, as the shipworm does in wood. Then there are sea-urchins which by unknown means excavate little hemispherical chambers for themselves in rocks; and rock-boring worms; and even seaweeds which use acid to excavate homes for themselves in limestone.

The boring habit is by no means confined to water-animals. There are no rock-borers on land, but wood-borers are numerous enough, almost all of them being insects. Though many of these feed on the wood they eat, yet none do so unaided; they all depend on the chemical activities of bacteria or protozoa, which they carry about with them inside—a specialist kitchen-staff. Many other insects once reputed wood-devourers have now been shown to feed on the moulds and other fungi which grow on the damp walls of their burrows. But whether they use the wood or no, they one and all inflict damage, whether they be termites or beetles, moth-caterpillars or wasp-grubs, and the damage is sometimes serious.

But we are getting away from the sea, and before we leave it for good we must speak of one curious group of creatures —the lazybones of marine-life that get carried about free of charge and effort. Floating objects will naturally be covered with the same sort of creatures as grow fixed on more stable hard surfaces; yet the landsman is always amazed when he sees the mass of creatures that succeed in growing on a ship's bottom within the space of a year or two, so dense that they cut down her speed by ten or twenty per cent.

Prominent among these foulers of ships are the goose-barnacles; these, though they grow on piles too, seem to have been specially evolved to hang down in the water from floating bits of wood. Big fish and turtles and whales are, from the point of view of such hangers-on, merely bits of floating substance which have the advantage of moving quickly; and they, too, are often covered with uninvited guests. In particular, the habitat provided by whales is sufficiently different from other floating habitats to have some unique inhabitants. There are certain kinds of giant acorn-barnacles which live exclusively there, anchored in a special way in the leathery skin.

But the most famous of all these passengers is the sucker-fish or remora. This carries on its head a powerful sucker, produced in the course of evolution by the transformation of its back fin. With this it sticks itself on to big marine creatures, usually sharks, and is whisked from place to place, detaching itself when the shark makes a kill, to feed on the fragments. So tight does the remora stick that in several parts of the world man makes use of it to catch fish and turtles for himself. Professor Haddon has given an interesting account of this method of fishing among the natives of Torres Straits. First you catch your remora; you attach it to your boat by a string through the base of the tail, and then proceed in search of turtle. When you see one, you creep softly up, and throw your remora towards it. The remora, prompted by its violent instinct of attachment, darts for the turtle and fixes itself to the shell. If the turtle is smallish, you simply haul it in; if bigger, you may yet have a chance of spearing it.

One final point about the sea as habitat: it is singularly bare of insects. A few spend their larval lives in it; and there is one solitary species of fly which spends its whole life in salt-water. It is the only region in the world of life, except for a few cold and snowy wastes, where insects are not one of the major groups.

CHAPTER III

LIFE IN FRESH WATER AND ON LAND

§ 1. Fresh-water Life. § 2. The Life of Flowing Waters. § 3. The Life of Standing Waters. § 4. Land Habitats. § 5. The Desert. § 6. The Tropical Forest. § 7. Regions of Rock, Snow and Ice. § 8. Island-dwellers. § 9. Cave-dwellers. § 10. Out-of-the-way Modes of Life

§ 1

Fresh-water Life

MASTER EVERYMAN, when he visits the country, likes to lean over the sides of bridges and watch what is going on below the surface of the moving stream. And his interest in brooks and ponds sometimes distresses his parents. But he is fascinated very powerfully by the unfamiliar world that exists under water. As he grows up, the pressure of earning a livelihood, the growth of other interests, the restrictive hedgings of convention, are more than likely to snuff out this healthy and natural curiosity, which is the necessary basis for science. Let the boy indulge in it while he can.

Meanwhile, what does he see from his bridge? He sees plants that trail and swirl instead of standing firm and erect; he sees occasional fish dart from one hiding-place to another, or use their tail-propeller to poise stationary in full current. There are water-snails, different in shape from the snails of land; in the quiet backwaters and eddies near the bank the whirligig beetles whirl and the water-skaters precariously skate on nothing but the water's own surface-film.

On the bottom are little caddis-worms, slowly crawling about with their houses on their backs—houses they have made for themselves out of sticks or shells or little stones. If he is lucky, he may see the larva of a dragon-fly or a may-fly crawling out of water on to a rush, bursting its skin, and escaping, a winged and aerial creature.

And then he goes to his favourite pond, armed with jam-jar and little muslin net. The surface is half-covered with a green sheet of duckweed—a plant that has reverted to the lowly condition of a mere plate of green tissue—and starred with white flowers of water-crowfoot. With his net he picks out a stickleback or two, and some handsome newts with their black-and-orange bellies. Then there are magnificent great water-beetles, smooth and shiny, stream-lined like a submarine, and provided with oar-like legs; and unpleasant creatures half-way between a grub and a small Chinese dragon, with formidable sickle-jaws, which, though he does not know it, are the larvæ of these same water-beetles. He catches plenty of water-boatmen, which he notices (he is an observant lad) prefer to swim upside down, and is lucky enough to find a water-scorpion. Snails' eggs in transparent jelly-masses there are in plenty on the water-plants; the newt-tadpoles with their feathery gills are growing up; and the place is teeming with just-visible water-fleas.

It is indeed a strange world, and a varied world, this world of fresh-water life; and Master Everyman could go on exploring it for long years without exhausting its surprises and its interest. And yet it is but a pale shadow of marine life. The chief reason for the lesser variety of the life of inland waters is that many aquatic phyla and classes have never succeeded in quitting the sea. Only a few groups of water-dwellers, like the aquatic insects, the ciliates and the rotifers, are more abundant in fresh than in salt-water, and one only—the amphibia—is wholly non-marine.

Life in fresh water demands certain special adaptations which not every group of animals has been able to produce.

The restricted size of most bodies of fresh water is unfavourable; whales or giant jelly-fish or the most active type of pelagic fish could not very well thrive even in large lakes. The small amount of salt in the water creates another difficulty. Blood contains salt as one of its most necessary ingredients, and wherever blood comes in close relation to fresh water, as in the gills of water-animals, there is a tendency for salt to leak out and for water to leak in. In amœba we saw a special structure, the contractile vacuole, everlastingly baling out water from the microscopic inside. In frogs and toads, the kidney has undertaken this duty; if a frog's ureter is blocked, and the animal is then immersed in water, it swells prodigiously. Bony fish have the power of keeping their blood-concentration almost constant in spite of variations in the salt content of the water, and hence are well represented in rivers and lakes; but in the gristly fish the blood alters with the surrounding medium, and, accordingly, sharks, dog-fish, or skates are almost unknown in fresh water. The absence of salt also means a lower density, and this (as any bather knows) makes it more difficult for free-swimming and free-floating creatures to keep up; as a result, we find that the average and especially the upper limit of size of fresh-water plankton is much below that of marine plankton (pp. 32, 33.)

Changes of temperature are in general more extreme in fresh than salt-water, so that no animals which are intolerant of wide alterations of heat and cold can hope to leave the seas. Again, the danger of being carried away and down to the sea is ever present in rivers and in most lakes; and when that possibility is absent, there is often the danger of drying up or of rapid rise in salinity. In all these respects fresh water is a more exacting environment than the sea, and many of the sea phyla have altogether failed to spread from their original home up the rivers into inland waters. But in contrast to this comparative poverty of primitively water-living creatures, we find that the so-called secondary aquatics—animals or plants which have

FIG. 12.—FRESH-WATER CARNIVORES.

Three water-beetles which use the hind pair of legs as oars, eating a small fish. Inset, the larvæ of two kinds of water-beetles; left, the Hydrophilus grub feeds on pond-snails and eats them under water; right, the Hydrous larva catches its prey under water but lifts it into the air to eat it. Both obtain air for breathing by pores at their hind end.
(*Inset from "Concerning the Habits of Insects," by Prof. F. Balfour Brown, Cambridge University Press.*)

gone back to water after a period of land-life—are much more abundant and varied in fresh water than in salt. Any land-creature has learnt to overcome difficulties even more severe than those we have just considered, and after its arduous training, finds fresh-water life comparatively easy. Moreover, that such secondary aquatics should prefer fresh waters to the sea is perhaps to be expected, since for one thing they are not so over-crowded with life, and for another the extent of shore-line inviting the evolutionary plunge is much greater, in spite of the total volume of water being so much less. There are plenty of secondary aquatics in the sea—whales and dolphins, seals and turtles, plants like the abundant eel-grass; but they make only a poor show compared with those of fresh water—all the cohorts of fresh-water insects, spiders and mites, fresh-water snails, fresh-water lung-breathing vertebrates such as newt and crocodile and terrapin, and all the innumerable flowering plants of fresh water—water-lilies and water-crowfoot, lotus and arrow-head, pond-weed and bladder-wort.

The main reason why a number of land-vertebrates have taken to fresh water (the reason holds for hardly any which have taken to marine life) is to escape terrestrial heat and terrestrial enemies. Such creatures often have the shape of their head modelled in adaptation to their amphibious life; nostril and eye are raised on protuberances so as to be above the water-line when the animal is floating—one has only to think of the silhouettes of frog, crocodile and hippo. The conning-tower and periscope of submarines are analogous devices of man's contriving (Fig. 13).

The smallness of most bodies of fresh water is an important factor, for it leads to their being frozen when the inexhaustible sea would be merely cooled a trifle, dried right up when the sea would evaporate a fraction more from its surface. And this has imposed remarkable powers of self-protection on many fresh-water creatures. In temperate regions, they usually tide over the winter by means of a resistant resting-phase, which may be egg or gemmule, seed

or pupa. Frequently, the need for a resistant winter stage together with that for the utmost possible utilization of summer's warmth has led to a remarkable type of life-cycle, in which generations of nothing but females, all parthenogenetic, succeed each other throughout the summer, while autumn brings males and sexual females, which produce fertilized "winter eggs," hard-shelled and cold-resisting, which will only hatch out in the following spring. This

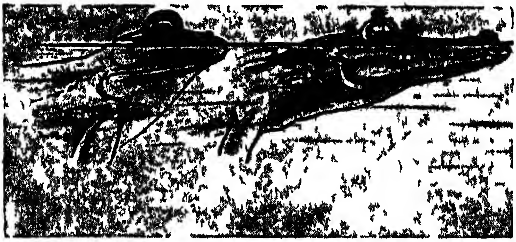

Fig. 13.—The Fresh-water Profile.

Frog, crocodile and hippopotamus all raise their eyes and nostrils on protuberances to be above the water-line when they float. (*Modified from R. Hesse.*)

type of life-cycle is found among rotifers and in two separate groups of crustacea; but it occurs only among their fresh-water forms. Certain full-grown rotifers can be frozen solid and remain for a very long time in cold storage without taking harm. Some which were thawed out by the Scott Antarctic Expedition could not have been less than five years in this state of suspended animation.

In many small crustacea, inhabitants of small pools in dry climates, the fertilized egg is not cold-resistant but

In fact, in some cases a preliminary

thorough desiccation of the eggs appears to be necessary if they are to develop at all. Many rotifers, on the other hand, as well as most tardigrades (bear-animalcules), and of course many Protozoa, can be desiccated entire even when adult, and will yet revive again on being moistened. These remarkable resistances to freezing and drying are not present in any marine animals—they are not wanted in the sea, there is no selection in favour of them, and so they have not been evolved.

The smallness of fresh waters has another important result, for it means that (except for a few vast lakes) they do not provide enough room for considerable waves to develop. This and the shelter afforded by banks mean that the surface of fresh waters will often be smooth, and this in its turn has encouraged the development of animals and plants of a type almost unknown in salt-water, which live in relation to the surface-film. Some of these manage to live wholly in air and support themselves on this fragile watery skin, some suspend themselves from it down into the water, and a number live actually in it, their top-half out of water, their bottom-half in. Among plants, the duckweeds are the most completely adapted to this border-land existence, but all the forms, like water-lily and lotus, in which the upper surface of the floating leaves is dry, belong to the same general type. Among animals, the whirligig beetles live most of their active life in the film, so much in it that their eyes are divided into two parts, the upper adapted for seeing in air, the lower for seeing down into the water; and the water-measurers actually treat the surface pellicle as a floor, and can skate over it dryshod, merely dimpling it with their feet. Many water-snails, on the other hand, even quite large ones, can use the surface-film as a ceiling, clinging to it with the surface of their foot and crawling along it; and Hydra may sometimes be seen doing the same thing. The eggs of many gnats and mosquitoes float in a raft in the surface-film; their larvæ, while they breathe, suspend themselves from it by means of a star-shaped set

of plates at the end of their breathing-tube; and when their pupæ moult into winged adults, these are only saved from drowning by being able to support themselves on the film as they struggle out. Almost the only creatures of the sea's surface-film are certain siphonophores, like Velella, with sails sticking up into the air, and polyps and tentacles dangling downwards into the water, and a marine water-measurer, the sea-strider Halobates, which may skate over the waves to quite a distance from land.

In connection with this life between air and water, we meet with further adaptations. The South American Jaçana, a bird related to the moorhen, is adapted to walk over lily-pads to find its food. For this purpose, its toes are enormously elongated, to spread its weight over a greater surface of leaf, as skis or snow-shoes spread weight over a greater surface of snow. And there is Toxotes, a tropical fish, which stealthily stalks insects sitting on water-plants, and then shoots at them with a rapid jet of water from its mouth. The insect, thus brought down to the water, is held struggling there by the surface-tension of the surface-film, and is promptly swallowed.

These creatures again remind us of the fact we stressed at the beginning of this section—that fresh-water animals and plants are highly specialized. The original home of life is the salt sea; to become adapted to living in saltless waters is itself an achievement.

§ 2

The Life of Flowing Waters

One general characteristic of all running waters is that they have no true or permanent plankton of their own. Plankton is constantly entering rivers from below at their mouths, and from above out of lakes; but it cannot colonize them. Plankton from the sea cannot swim upstream; plankton from the lakes is all, sooner or later, swept out to

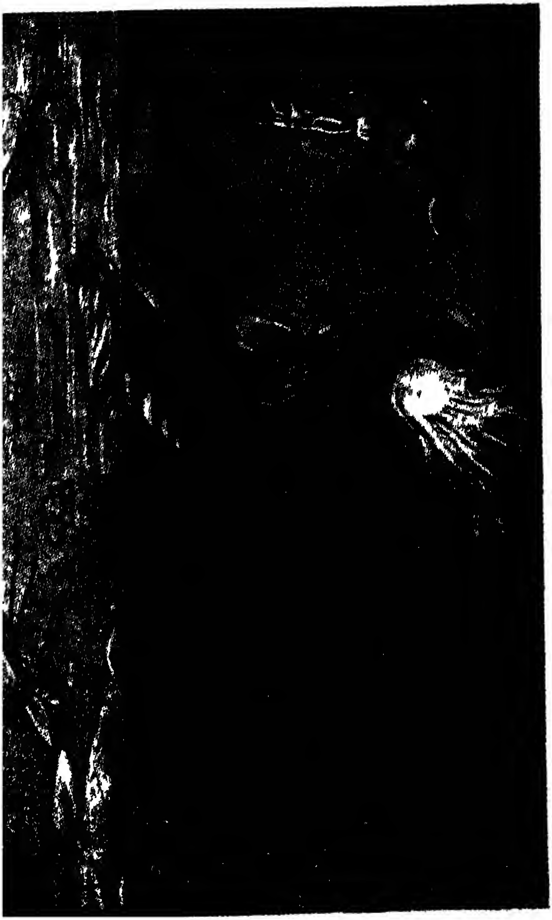

FIG. 14.—POND-LIFE AT THE SURFACE-FILM.

Water-lilies send up their leaves to rest on the surface; duckweed plants float there, with roots hanging down. Water-measurers skate on the film; a water-scorpion, several gnat pupæ and larvæ, and a water-beetle larva (seizing a tadpole) poke their breathing-tubes through it. A small water-beetle carries down air under his wing-cases, a water-spider (centre) transports air with which to fill its waterproof nest. Whirligig beetles swim in the film; a pond-snail crawls on it upside-down, as if it were a ceiling.

sea. The open water of rivers is not in itself in any way unfavourable to the growth and multiplication of plankton —the small crustacea and especially the quick-generationed rotifers from lake-plankton may grow and reproduce through several generations when swept into rivers; but all this multiplication is pure waste as regards the species, although, of course, it may serve in feeding other creatures. This source of food may be important; where the waters of the Elbe are slowed down on entering its estuary, over ten million plankton crustacea may be found in every cubic yard of water. All these millions of creatures will eventually fall from the tree of the species, to be replenished by fresh accidental immigrants from above. The one fact of flow has prevented the rich open water of rivers from possessing its own fauna.

Indeed, it is rate of flow more than any other single factor which moulds river-life. Fast-running water hides animals under stones, robs them of the hairs and bristles by which small limbs become swimming paddles, flattens them, stream-lines the contours they expose to the rush of water, causes them to grow suckers or other adhesive devices, or even forces them to ballast themselves with stones to prevent them being washed away. Moreover, such little larvæ as serve for dispersal purposes in the sea are absent in flowing waters. The first stage of the marine polyp Obelia is a tiny ciliated oval; swimming independently about that of the fresh-water polyp Hydra spends the same period of its career in a heavy egg-case on the bottom. The lobster or the prawn passes through a juvenile open-water phase; the river crayfish develops as an embryo clinging to its mother's abdomen.

On the other hand, while swift water encourages animals to temporary attachments and wedgings away into chance crevices, it discourages all forms of permanently fixed habit, for the reason that the bottoms of swift rivers are largely composed of loose stones which, tumbling over and over, afford no permanent abode themselves, and would crush

most organisms growing on rock; and, further, food is so scarce or so rapidly carried past (or both) that animals cannot afford to be tied to one spot. In the swift streams of temperate Europe, only thin crusts of one kind of fresh-water sponge and occasional colonies of a polyzoan are found in place of the sea's horde of stalked animals. Since plants cannot develop temporary anchors, and yet are exposed to the same violences of current and down-driving stones, they too are only poorly represented in rapid streams.

That it is the speed of the water, not the size of the stream, which is chiefly responsible for these adaptations is shown by the fact that when giant rivers, like the Congo or the Essequibo, have stretches of rapids on their middle course, the fauna and flora show adaptations of precisely the same nature as those found in a Westmorland beck or a Swiss torrent.

In streams with gentler flow, these adaptations are not necessary, and are not found. When the flow is very slow, slow enough to allow the deposition of fine sand or mud, a special fauna arises to exploit this bottom layer, and may show some remarkable adaptations. Aquatic bristle-worms like Tubifex, Limnodrilus and Lumbriculus, which resemble miniature earthworms, may occur in vast quantities in such localities. In the Elbe below Hamburg, about 27,000 of such worms may inhabit one square foot; at low tide in central London great patches of the mud can be seen coloured dingy red by Tubifex. These worms often construct tubes for themselves. They bury their heads at the bottom of these pipes, and eat the slime; the tubes stick up like chimneys above the mud-surface, and from them project the posteriors of the worms, waving rapidly to and fro to facilitate respiration, which is carried on, not only by the surface of the body, but also by rhythmically passing water in and out of the hind-gut through the anus. They are, like earthworms, constantly eating their habitat, digesting the nutritious bits from it, and ejecting the rest as castings. Their activity in this respect is prodigious; a Limnodrilus

an inch and a half long may produce five feet nine inches of fæcal castings in the twenty-four hours! The huge numbers of worms thus continually bringing up new material to the surface, where it can be readily oxidized, play valuable rôles in purifying foul water.

Other slime-feeders, which may even exceed these worms in bulk per unit area, though not in numbers, are little bivalve molluscs. In other parts of the lower Elbe one of these, Sphærium by name, abounds to the extent of nearly 7,000 per square foot.

In less muddy regions, the predominant river-animals are insect larvæ. Everyone knows the dense swarms of mayflies that hover over our rivers for a brief spell in early summer. Their adult existence is brief, never more than a week, sometimes only a single day, for their mouths never open and they cannot feed. They have lived all their previous life of one, two, or even three years in burrows in the banks. Many of the alder-flies and dragon-flies and scorpion-flies have river larvæ too, so that the number of insects whose main food-supply is found in rivers is a very large one.

All such abundant small animals, at some stage of their career, afford rich food to larger forms. Of these the most important are the fish. Here, among fresh-water fish, we are able to trace with beautiful clearness, not only certain definite adaptations to fresh-water life, but the way in which increasing difficulties of adaptation weed out more and more of the competitors for existence.

Rivers may be divided into sections according to their dominant fish. In Europe, the head-water region, with swiftest flow and clearest water, is characterized by the trout, with minnows, miller's thumb (*Cottus gobio*) and loach (*Cobitis barbatula*) in attendance. Below this is often a zone with dominance of the grayling (*Thymallus vulgaris*), and then the barbel region; or this latter may immediately succeed that of the trout. Then comes the quiet-flowing domain of the bream; and down-river from this the estuarine

region, with stickleback and smelt as most prominent members, pike and eels in its upper, less salty zone, and flounders and, in some rivers, sturgeons in the zone nearest the sea. These regions do not always succeed each other in this precise order, since streams may for instance have a region of rapid flow and pure water, and therefore of trout-fauna, intercalated on their middle course. But the order holds as a general rule.

Now as we go up from the river-mouth, in the first place the habits and the body-form of the fish change. Flat-fish never go far up the rivers, since food-rich bottoms of clean sand are absent. The chief estuarine types are those, like sticklebacks, adapted to rapid changes in salinity, or, like eels, to a muddy life. Above this stretch, within the true river, the shape of the body changes steadily with increasing rapidity of current. In the lower reaches are forms with poor musculature and sideways-compressed body. In more rapid currents, more muscle is needed to keep up, and the body must be more rounded so as to expose less surface to the flow of water. At the same time, the proportion of mud-rooters diminishes, the proportion of those which prey on tit-bits floated down in the current increases.

And finally the number of species diminishes. The number of fish species in the Rhine is as follows: In Holland, 41; in the upper Rhine just below the falls, 28; above the Lake of Constance, 25; up to 700 metres above sea-level, 11; up to 1,100 metres, 5; to 1,900 metres and over, only 3 (trout, minnow and miller's thumb). And similar figures may be found in other rivers all over the world.

Perhaps the most remarkable of river-fish are the migratory members of the salmon family, which feed and grow in the sea, but for their reproduction migrate up rivers, often for hundreds or even thousands of miles, to the shallow head-waters, where in "redds" scooped in the gravel, under the well-oxygenated water, the eggs are laid and fertilized. Sometimes the great fish crowd into such shallow waters that they are scarcely submerged. In Alaska even bears

and their cubs come to the brooks in salmon time and scoop the creatures out of water with their paws. In some species of salmon the spent fish may drop down to the sea again; but in others, not one of all the swarms which enter fresh-water survives; they make the great journey but once in their lives, and die when its biological purpose has been achieved. During all this time the fish seem to eat nothing, and their stomachs are contracted and secrete no gastric juice. All the energy for the journey and much of the materials for the development of sperms and eggs are obtained partly from the reserves of fat and muscle-sugar in the tissues, and partly at the expense of the living flesh itself, so that the fish are left in a very emaciated state after spawning.

Considerable dispute has taken place as to whether the salmon family were originally fresh-water fish which have taken to marine feeding because of the greater abundance of food to be obtained in the sea, or marine fish which have taken to fresh-water breeding on account of the greater security provided to the eggs and young fry. But the latter view is in all probability true; so that permanently fresh-water species like the trout are degenerate or at least specialized forms which have secondarily ceased to migrate.

The incredible concentration of these fish in the early spawning season at the entrances to rivers makes the salmon fishery the most important of all river fisheries. In Canada alone, the value of the Pacific salmon caught in 1922 was thirteen million dollars.

Sturgeon and their relatives behave exactly as do the salmon, and like salmon, they are captured while on their long pilgrimage of reproductive destiny and turned to human profit. Fresh-water eels, on the other hand, execute a breeding migration in the opposite direction, as Kingsley has vividly described in his *Water Babies*. In early autumn the mature eels, leaving the quiet ponds where they have lived and fed for years, and often crawling a mile or more across wet grass in the cool night to reach the nearest stream, make their way down to the sea. In preparation for this

migration, they change their whole appearance, and from what fishermen call "yellow eels" become "silver eels." Their bodies grow silvery, their eyes enlarge enormously, their snout becomes pointed, their reproductive organs swell, and they cease to feed.

On reaching the sea, the eels are led by some mysterious instinct towards their distant breeding-places in the depths. English and Scandinavian eels, and even those from the recesses of the Baltic, travel across the whole Atlantic to the borders of the Caribbean Sea, where, at unknown depths, they spawn. The eels of Eastern North America, though of a different species, spawn close by. Those of Mediterranean countries spawn in the deeps off Sicily. The object of their pilgrimage thus attained, the creatures all die.

The eggs hatch into transparent leaf-like creatures, at one time thought to be a distinct genus of fish, and described under the name of Leptocephalus—"thin-head." These migrate slowly homewards, feeding and growing all the while. Johannes Schmidt has mapped them by their size, and by this means was able to show where the breeding-place must lie. Eventually, when about three years old, and two inches and a half to three inches long, they metamorphose rapidly into a miniature eel or elver, shrinking considerably as they do so, and swim in dense hordes into the mouths of rivers, where they are often caught by the bucketful for food. The American eel is more of a hustler: it metamorphoses before it is two.

There can be no doubt that eels were originally marine. The conger eel is wholly marine, and it too breeds in the deeps and has a similar leaf-like larva. So that the fresh-water eel is the reverse of the salmon. It has kept to its original deep-water breeding-place and feeds in fresh-water alone. Both salmon and eel have taken advantage of their adaptability to penetrate from the sea to waters where there is less competition, but they exploit fresh-water for different purposes.

A lamentable feature of our industrialized world is the

way in which it pollutes its rivers. Sewage; the poisonous run-off of certain kinds of tar on roads; chemical effluents of every description—they turn our streams filthy and turbid and destroy the best of their life. The prevention of pollution is a complex problem, with its economic as well as its biological sides, and we cannot enter into it here. But we can drive home the facts with the aid of a single example. The sewage and the chemicals in the Thames to-day would kill any salmon that tried to swim up or down its lower course. But less than two hundred years ago, the Thames was a good salmon river. And in the thirteenth century, the Thames at London was so full of fish that when Henry III was presented with a polar bear by the King of Norway, it was kept at the Tower of London and allowed to swim about at the end of a rope and supplement its allowance with the fish it could catch.

§ 3

The Life of Standing Waters

The life of fresh-water that is not moving is very different. There is no hurrying flow to inhibit plankton and larvæ or to insist on firm anchorage, and the size of bodies of standing fresh-water may be so great as to permit a regular stratification of open-water life by depth, in faint imitation of the sea's vaster economy.

Lakes, owing to the physical properties of water, rarely freeze solid. Pure water is densest at 4° C., not (like almost all other liquids) at its freezing-point; thus, in winter, after the whole mass of water has been cooled to 4°, further loss of heat from the surface will leave a cold layer of temperature lower than 4° floating on the rest; this will freeze, and, owing to the poor heat-conductivity of water, further chilling of the air will cool the lower layers but slowly. If, as with most liquids, the density of water steadily decreased to its freezing-point, a circulation of the lake-water

would take place until all was at 0°, and then the whole mass could freeze almost at a bound into a solid block of ice.

As a result of this peculiarity of water, organisms can survive through the winter under the lid of ice, doubtless in a torpid or semi-torpid condition owing to the low temperature, but without having to develop special adaptations against damage due to the freezing of their tissues. Since no vertebrate animals are known which can survive long-continued freezing solid, it is probable that if it were not for water's peculiar property of being heaviest at 4° C., there would be no fresh-water fish or amphibia in existence, or at least none whose adult life surpassed a single season. This property of water is one of the central themes in L. J. Henderson's interesting book, *The Fitness of the Environment.*

In all deep lakes in temperate regions the bottom water will be permanently at 4° C. Twice a year, in spring and autumn, the whole of the lake will be at this temperature. But the surface water will be the warmest layer in summer, the coldest in winter.

The plant-inhabitants of a lake margin are for the most part an invading army, taking possession of this vacant but difficult territory under stress of terrestrial competition. As the water deepens, the invaders change their tactics. Near the edge they are merely paddlers, with only the roots and a little of the stem below the surface. Farther out they must wade, and (to keep the animal metaphor) must grow longer legs, like any heron or flamingo. Some become amphibious, with part of their foliage below water, though the plant as a whole is still constructed on principles taken over from land-life. Deeper yet, and the whole plan is altered. Still clinging to air, the drowning plant sends up leaves and flowers to float at the surface at the end of stalks that are no longer supports but mere flexible mooring-cables and transport-conduits. Such are the water-lilies. Finally, the deepest venturers discover that submersion need not mean drowning, and like the pond-weeds, alter the

whole structure of their leaves so as to be capable of food-manufacture and breathing under water.

It is more difficult to re-adapt reproductive methods to a submerged life; the dry dusty pollen, evolved during æons to be floated on the wind or to powder the hairy heads and backs of insects, does not take kindly to a wetting. Some plants whose vegetative life is all submerged, like the pond-weed Potamogeton, still send their flower-shoots up into air; the famous Vallisneria detaches its male flowers while still closed; these float up to the surface and open; the sepals bend back so as to raise the anthers to the level of the stigma of the female flower, which, meanwhile, has been paid out to the surface at the end of a long thin rope of a stalk. The male flowers, drifting hither and thither, may come to rest in the little harbours between the sepals of the female flowers, and then some of their pollen gets rubbed off against the stigma. Once the female flower is pollinated, its stalk contracts into a spiral and pulls it down to safety near the bottom.

A few plants, however, have adapted their reproductive as well as their vegetative life to water. Naias, a relative of the marine eel-grass Zostera, forms pollen-grains without the usual outer coat, and elongated and thread-like instead of rounded in form. These are discharged under water; their large relative surface helps to float them, and some drift into contact with the stigmas, which, too, are submerged. Accordingly, Naias and its relatives extend to greater depths than other secondary aquatics among plants, being released from all need of contact with the air; they are only limited in their downward invasion by the diminution of the light as it filters through the water.

Besides these secondary water-plants, there are, of course, others (such as Spirogyra and other thread-algæ) which have been aquatic throughout all their history. None of these, however, attain in the fresh-water community anything like the size or the importance of their marine congeners the seaweeds.

The animals of lakes are also perhaps best classified into the secondary invaders of water and its permanent inhabitants. The latter, save for one group, are less important than the former in size and variety. They are largely composed of small creatures belonging to groups from the lower crustacea downwards—water-fleas, shrimplets, rotifers, the little cœlenterate hydra, fresh-water sponges, flatworms, and protozoa. The secondary invaders, on the other hand, include all the thousands of insects which live in water either all their lives, like the great Dytiscus beetle and the water-boatmen and water-scorpions; or through all their growing larval existence, like the may-flies, caddis-flies, stone-flies, and the great dragon-flies, falcons of the insect world. They include also frogs, toads, salamanders and newts during a certain season each year of their adult life; also most water-snails, and all the water-birds. These last are more bound to land and air but, like the plants, throw out representatives to ever more aquatic life, from paddlers like the sandpipers to waders like the heron, and so to swimmers; and the swimmers become more and more bound to their medium as we pass from surface-feeders like moorhens and gallinules and bottom-grubbers like the swan, on to divers like the diving ducks and the grebes.

The single exception to the dominance of secondarily aquatic forms in lakes is an important one—the fish. Whereas the economically important river-fish are mostly wanderers to or from the sea, those of lakes are home products, and some lakes, like the Caspian and the Sea of Galilee, provide vast quantities of food to the neighbouring countries.

In general, the plankton of lakes is much less well-developed than that of the sea, and as direct consequence of this, active pelagic fish are less abundant, bottom-feeders more abundant than in the sea. Among the few plankton-feeding fresh-water fish are various members of the salmon family, such as the different species of white-fish (Coregonus) and some lake-trout. As most of the bottom of

lakes is covered with fine slime, in whose nutritious lap live abundant insect larvæ, worms and bivalves, many of the bottom-feeding fishes are provided with long whisker-like feelers, with which, as a matter of fact, the fish can not only feel but also taste; and also adaptations in the shape of the tail (as in the sturgeon) or the backward prolongation of the ventral fin (as in some of the catfish) which serve to force the head down in its rootings among the mud.

The large plant-plankton, as in the sea, consists largely of diatoms and peridinians; but again as in the sea, the dwarf-plankton, which passes through the meshes of the finest net, is even more abundant.

The animal-plankton of lakes comprises for the most part small crustacea and rotifers, and besides that a few water-mites and protozoa; but very few insects have become so completely readapted to aquatic life as to have taken to open water and to the peculiar feeding methods there needed. Though the plankton may be abundant, yet even in quantity it falls below that of cool seas; and in variety it is infinitely inferior. One or two interesting plankton animals deserve mention, notably the little glassy carnivorous crustacea, such as Leptodora.

In the great majority of lakes, in consequence of their smaller depth and their smaller geological age, there is practically no special deep fauna or flora. It is only in a very few large, deep and comparatively ancient lakes, like Baikal in Siberia and Tanganyika in Central Africa, that a real deep-water world of life exists. In other lakes there may be deep-water forms, but they are ubiquitous creatures found also in the shallow zones, and have not had time—since most lakes are geologically very short-lived—to become specially adapted to the peculiar habitat. But in Baikal, for instance, at about 600 metres depth there are gammarid crustacea which are blind and have antennæ and limbs elongated as feelers, and fish like Comephorus, which has lost almost all its pigment and is a shimmering pink. In Baikal, the gammarids are the dominant group of crustacea,

and have launched out into all sorts of peculiar ventures. The same sort of thing has occurred with the fish of Tanganyika: over half of its 150 species of fish belong to one family, the Cichlidæ, and the great majority of these are products of Tanganyika evolution, found nowhere else in the world.

But we have devoted our attention long enough to the inhabitants of watery worlds. It is time we turned to the creatures of land and air.

§ 4

Land Habitats

There are only a few groups of animals and plants which have succeeded in invading the land. Here perhaps we may add a note on the reasons which prevented animals of certain other types of construction and ways of life from succeeding. First the net weight of an organism in water is negligible. In sea-water, protoplasm weighs only about a thousandth of its total mass; even in fresh-water, only about a two-hundredth. But in air, weight counts. And so all animals and plants without some means of mechanical support are debarred from terrestrial life. No jelly-fish can conceivably be imagined which could successfully invade a land habitat. There are a few land-animals that lack a skeleton. But in these, earthworms can only exist *in* the soil; and land-planarians are confined to hot, moist places. Slugs and land-leeches are the most successful of such creatures; but they both need a dampish atmosphere. Each is, however, in its own way, successful. The slugs are serious enemies of the gardener; and in some parts of the tropics the armies of land-leeches, attached to the vegetation and constantly waving their bodies about in search of possible prey, are among the most unpleasant pests with which explorer and pioneer have to contend.

And, secondly, no creature whose whole life is adapted

to current-feeding can become terrestrial. Even if (as is probably impossible) the current-producing cilia could become adapted to beating in air instead of in water, there is scarcely any floating assemblage of living things or their debris to be captured from the air, since, weight in air being what it is, all particles above a minimal size sink at once to the ground. For this same reason no sedentary animal which merely spreads its tentacles for prey can live on land. The tentacles would collapse and the abundance of prey is not there. Only much later, by new devices specially adapted to air and its inhabitants, have creatures like spiders exploited this catchment method of gaining a livelihood in terrestrial surroundings. This difficulty rules out from land-life the whole group of hydroid polyps, the jelly-fish and the corals; and the impossibility of current-feeding debars all the sea-squirts and other tunicates, the bivalve molluscs, polyzoa, lampshells, and lower chordates like Amphioxus.

No echinoderms have ever left the sea, although they possess a skeleton, and the free-moving types are not dependent upon current-feeding. On the other hand, their whole locomotion depends upon hydraulically-operated tube-feet, which could not easily be made over so as to work in air.

The substitution of protected stages of seeds for free-living stages and embryos for larval forms, in the life history, is one general rule of aerial adaptation—to which only the insects furnish exceptions.

The habitats open to life on land are more varied than in any other medium. But many of them are already familiar to Mr. Everyman, in virtue of the fact that he is himself an air-breather. Though he does live in a town, he has visited various parts of the country, and so (like Monsieur Jourdain, who found he had been speaking prose all his life without knowing it) has unconsciously imbibed a knowledge of the chief land habitats of temperate regions.

He has walked over the close-cropped downland, and

the rich water-meadows. He has seen the hares (the mad March hares) chasing each other in spring over the open fields, and noticed that they avoid the woods. He knows the difference between a pine-forest and an oak-wood—the one permanently dark, carpeted with little save a thick brown layer of pine-needles, the other lighter and with a richer undergrowth, especially in the spring when the roof of leaves is not yet grown, and the primroses and wood-anemones and wood-sorrel cover the floor of the wood with blossom.

He knows the barren sandy heaths, alive with rabbits, bright with purple-flowered heather in July and yellow gorse in spring; the meadow-pipits sing there, and the nightjars lay their eggs on the bare ground. If he has visited Dartmoor, or the Lake District, or Scotland, he knows what a moor looks like, and has seen a peat-bog; he realizes that there are habitats so poor that trees will not grow on them, and can readily take the step in imagination to the more barren tundra of the arctic or the craggy regions of high mountain ranges. And yet these places, too, are full of beauty and of life; there are ravens and falcons in the crags, dippers by the streams, sometimes red-deer and mountain-hare, grouse or ptarmigan. The stones are covered with lichens; between them grow mountain flowers, smaller but often brighter than those of the low-lands.

Or he may happen to live in the Middle West of America; and then he will know the great sweep of the prairie, covered with flowers in spring, growing into a sea of grass later in the year.

If he has any curiosity and interest in natural history, he will know something about the commoner land plants of his country, the commoner land beasts, birds, insects, and other animals, and where and how they live. Comparatively few people know by personal experience what a jelly-fish or a spider-crab, a sponge, a sea-cucumber or a cuttle-fish look like in their natural surroundings. But

they inevitably have some acquaintance with rabbits and robins, bees and beetles, spiders and slugs, snakes and frogs and earthworms.

We cannot deal with all the diversified habitats of land in detail; many of these more familiar ones we shall leave out, or will deal with certain aspects of them only, in later chapters. Here we will take a few of the more striking of the contrasted habitats of dry land, and those that are likely to be unknown by personal experience to most of our readers, in order to bring out the salient facts of life's adaptation to land.

§ 5

The Desert

We may begin with the desert, since this possesses in exaggerated form all the characteristics which made the land hard to colonize. Botanically, the desert is at the other end of the scale from the tropical forest. In the equatorial forest, all that a plant can desire is provided; the difficulties arise not from the harshness of the surroundings, but from the fierce competition due to the very ease of growth. In the desert, on the other hand, the soil is at the best of times not fully exploited; the desert plants provide an extreme example of what ecologists call an open formation, with great stretches of barren plantless environment between the scattered units of life. There is little struggle between plant and plant, but intense struggle of organism with inorganic nature.

On our globe, a double desert zone exists, girdling the tropics on both sides. The great Palearctic desert embraces the Sahara and all of Egypt save the coast and the Nile valley; Sinai, Arabia, the Syrian desert; and so across parts of Persia and Afghanistan to Turkestan, Tibet and the Gobi, with a side-branch into Western India. The North American desert, including the celebrated Death Valley,

reaches across some of the south-western States and northern Mexico. On the other side of the equator there is a corresponding band of deserts in South America; in South Africa there is the Kalahari; and Australia can boast of the earth's second largest area of completely desert land.

It is difficult to define a desert meteorologically. In general, it is of course a place of heat and drought. The rainfall is usually low, very variable from year to year, and, if it does not fall in minute amounts which evaporate again before reaching the roots of the plants, is often confined to a few heavy bursts which run off before they can soak deep. Deserts are not only hot places; they are places with very great fluctuations of temperature, both yearly and daily. This is doubtless in the main due to the clearness of the sky and to the absence of vegetation and of water-vapour. With a clear sky, heat radiates unbrokenly in from the sun, out again into space; but a blanket of vegetation impedes the passage of heat into or out of the soil. Where plenty of water exists, much of the sun's heat is used up, without rise of temperature, in transforming water into water-vapour; the restoration of this latent heat during night-cooling again acts as a damper on rapid temperature-change. In a desert, this temperature-buffer is almost absent. In addition, water has a high "specific heat"; if we put the same amount of heat-energy into a pound of water on the one hand and a pound of dry earth on the other, the second will get hotter than the first. That is another reason why wet clayey soils are "cold," why the waterless soil of deserts heats up and cools down with such surprising rapidity. The result is that the night temperature may drop below freezing-point after a day maximum of 80° or 90° F. In many deserts the minimum temperature usually keeps just above freezing. But then, one year, there is a frost; it can be imagined what damage this will do.

In passing, it may be noted that merely irrigating a desert with water will not convert it to fertility. It works for a short time, but owing to the intense dryness of the air the

water evaporates very quickly, leaving behind it any salts it may have contained. These gradually accumulate in the soil, until the last state is worse than the first. This problem of the caking of irrigated desert soils with salt has already become acute in various regions, including parts of Egypt, and soil science is being hard put to it to find a way out of the difficulty.

Deserts are violent places. As there is no mist and hardly any water-vapour in the air, the intensity of sunlight is greater in deserts than anywhere else save perhaps the tops of high mountains. Not only temperature and rainfall, but also relative humidity and windiness show huge fluctuations. A North Sea gale is nothing compared with the gale experienced by the explorer Augieras in the Western Sahara, which lasted nine days, and was so violent that he could not stir the whole time from out of the lee of a sheltering rock.

We are accustomed to the two great cycles of day and year. Near the poles, the diurnal cycle drops out over a large part of the year. In some deserts, on the other hand, it is the yearly cycle which ceases to be important. Whole years may pass without rainfall, and there may be no regular relation between weather and season. Biologically speaking, the cycle of the year may cease to count in deserts; and only the long-range periodicities, such as the eleven-year cycle, of which we shall speak in a later chapter, with their disturbing effects upon earth's weather, make much difference to desert plants and animals.

In less extreme deserts, however, the seasonal cycle remains; there is a brief moist spring, and then indeed does the desert blossom like a rose. The bare soil comes to life, green shoots push up, burst into flowers that carpet the land with colour and bring with them as their biological attendants the hum and flutter of swarming bees and butterflies; the seed is set: and a few weeks later all has disappeared, and the bare soil, dotted with a few perennial thorns, alone remains. Cinderella's coach has been turned back

into a pumpkin, her lovely dress into dead leaves—only the change seems even more miraculous, for at first sight it looks as if the desert's beauty had vanished into nothing.

In reality, one half of the plant-life—the annuals—has retired into drought-proof safes, in the shape of seeds. The other half, the perennials, have their permanent being subterraneously, in living store-houses that we call bulb or tuber or fleshy root. In the few spring weeks they do all their year's work, of manufacture and reproduction alike, and then retire to vegetate invisibly below ground for the rest of the year.

But the most striking desert plants are the big fleshy water-storers. The most familiar of these are the cactuses, but the spurges (*Euphorbias*) and many of the composites of deserts have been modified in the same direction, often so thoroughly that all save experts mistake them for cactuses. The agaves and aloes and spanish bayonets show similar but usually less striking modifications. In such plants, the roots are generally deep, the tissues fleshy and built so as to be able to store large quantities of water in their cells. All plants must be constantly passing water from root to stem and leaf and out into the air as water-vapour; the current serves for vital transport; but in these desert plants its amount is, by one means or another, cut down. This enables them to draw water out of the soil during the rains and to store it for the hard times ahead. A hibernating bear or hedgehog lives through the time of food-scarcity on its piled-up stores of fat; a cactus lives through the time of drought on its stores of water.

The usual method for achieving this is by a great reduction of the surface from which water can be given off as vapour; very often, as in cactuses, the leaves are small and temporary, or even absent, and their work is handed over to swollen stems, which expose a much smaller surface to the air in proportion to their bulk. The climax is reached in the barrel-cactuses, which stand about in the desert like casks, and like casks are full of water; but their surfaces

are beset with wicked spines to protect the precious fluid inside from browsing animals. In passing, it may be pointed out that the plants that retire underground for the dry season and live as bulbs and the like are really doing something very similar, though more extreme, for they cut their transpiration-current down to zero during the drought; and those which bridge the dry season in the shape of seeds go one better, by getting rid of all their water and passing into a desiccated state of suspended animation.

In the perennials, which do not die down above ground, mere reduction of transpiring surface is aided by other adaptations—the cuticle is varnished over with wax or resin, or a thick coat of hairs checks diffusion, a layer of cork protects the stem-tissues from evaporation, or the microscopic plant-mouths through which the water-current vaporizes out are tucked away in deep pits on the under side of the leaves. Often, too, especially in salt and "alkali" deserts, the amount of salts in the cell-sap is very high; this holds water and makes it harder for it to evaporate away, while at the same time helping the roots to pull water out of the soil.

Spines and thorns are a frequent accompaniment of desert-life. Hedges of prickly pear are more impassable than barbed-wire entanglements, and are often used for military purposes in protecting forts and camps; and the spines with which the agave's leaves are tipped are really formidable stilettos. In part, spininess seems to be the direct outcome of dry surroundings; but the tendency in that direction has undoubtedly been improved upon by Natural Selection to protect the succulent tissues—often the only source of moisture for miles—from animals. In certain North African agaves the long leaves are tipped with black-brown, and suggest the same hardness and sharpness as the leaves of ordinary agaves. But in reality the tips are perfectly soft and flexible—dummy spines. Apparently we have here a case of mimicry among plants, analogous to

that of the dead-nettles which look like stinging nettles. The harmless plant gains an advantage by looking like a dangerous one.

The desert has the same dual effect upon life as have other habitats with a combination of special and very unfavourable conditions. It exercises a rigid selection upon immigrants; and it calls forth a number of special adaptations in those which are successful in entering in. No true aquatic animals can live in deserts, save in the sparse oases. Amphibia, with their moist skins, are almost all turned back at the frontier; and so are those other moist-skinned animals, land-leeches and land-planarians, and those groups of insects, such as may-flies and dragon-flies, which have returned to water for their growth-stages. Animals confined to a purely insect diet and incapable of flight are almost unknown in deserts, probably because insects are abundant only at one season. Owing to the general scarcity of life, large animals are absent; the maximum size diminishes as we penetrate from the half-desert or desert-steppe to the true desert heart.

As a result of this selection, the types of animals which make up the bulk of the desert fauna are those which were already provided with a dry skin and a wholly terrestrial life-history—beetles, butterflies, Orthoptera and Hymenoptera among the insects; centipedes, scorpions; and among vertebrates, birds, mammals and notably reptiles.

Those of other groups which have passed the immigration test have done so by means of special aptitudes. Land-snails are not unsuccessful desert forms; they owe their success to their power of closing the opening of their shells with a door of hardened mucus, behind which they sleep away the driest time. A few land-crustacea in the form of woodlice live in deserts; most of them have a high dome-shape, which reduces their relative surface. No tailed amphibia exist in any desert; but there are a few frogs and toads. In the Australian desert, four species are not uncommon. They are without any annual breeding cycle,

and can spawn immediately rain falls, whatever the season of the year. One species makes burrows down to the just-moist soil of torrent beds, and lays its eggs in a foamy mass at the bottom of its burrow; development proceeds within the egg to the early tadpole stage, and the eggs then wait for rain; when the rain comes, the eggs swell up, burst, and release the tadpoles, which grow rapidly and change into frogs. One form, called Chiroleptes, has taken a leaf out of the cactus' book, and stores water. An Australian observer writes: "If you put a lean dry herring-gutted Chiroleptes into a beaker with two inches of water, in two minutes your frog resembles a somewhat knobbly tennis ball." Absorption goes on all over the skin, and the water is stored not only in the bladder but in the sub-cutaneous tissue and the body-cavities, making the frog nearly spherical. The blackfellows, if hard pressed, use it as a source of drinking water. This is the only species of Amphibian which can live for long periods in completely dry conditions.

Another and very different adaptation to drought is seen in the sand-grouse. Those powerful fliers nest in the steppe-deserts of Asia, and the adults can quench their thirst by flying off to the nearest oasis, though this may be miles distant; but this the young cannot do. The problem of their drinking is solved by the parents soaking their breast-plumage in water, flying straight back, and allowing the nestlings to suck the moist feathers. However, a not infrequent adaptation to water-shortage is seen in the capacity which many desert animals possess of going without drink at all. They get all the water they require out of their food. Various desert mice and jerboas, and even some larger animals, such as gazelles, possess this valuable physiological power.

We have already spoken of the prevailing matching of the desert's sandy colour. Then there are a number of adaptations concerned with wind; we will mention two. Many ground-nesting birds build semi-circular ramparts of

stones to protect their nests from the prevailing winds. Without these defences, the nest and eggs would be in frequent danger of being buried by the sand which the wind drives along. An even stranger case is that of a small butterfly in the Syrian desert, as recorded by Buxton. If it lived in the open, it would risk being blown clean away by the gales that sweep over the bare country; accordingly it spends the whole of its life fluttering about inside one of the rare desert bushes!

Another problem is temperature. In many deserts the temperature of soil exposed to the midday sun is enough to roast eggs—a good deal higher than anything which ordinary protoplasm can stand; and even in the shade, the thermometer will often go up to 120° or 130° F. The most obvious adaptation is to go about your biological business by night: and, as a matter of fact, a high percentage of desert animals are nocturnal. Of the creatures of the day, almost all avoid the sun as much as possible. All mammals and birds can regulate their temperature, and in deserts they can, if need be, keep it below that of their surroundings, just as in colder places they can keep it above the outside temperature. But many desert reptiles, notably lizards and snakes, have special adaptations tending in the same direction, by means of which they can at least keep themselves a few degrees cooler than the oven-like world outside, and so save themselves from sudden coagulation and death. The usual method is for the animals to have a mouth-cavity richly supplied with surface blood-vessels, and to pant rapidly with open mouth. This, as in a dog that has been heated up by running, causes evaporation and consequent cooling.

There is one final aspect of desert life that should be touched on. The scanty, open vegetation means a shortage of food for animals, and they must adjust their population to the supply. Sometimes they lay up stores against the time of drought and scarcity. This habit is what attracted Solomon's interest in ants. The ant he held up as model

to the sluggard was an ant of dry climates, a grain-storer. Our more northern ants do not have the storage habit. Some desert mammals also store food: for instance, the kangaroo-rat, Dipodomys of the American semi-deserts. This little, agile, jumping creature makes big mounds, full of tunnels and chambers, and in these amasses huge stores of grasses, flower-heads, and the like. In one mound no less than 12½ pound of hay-stores, mostly valuable forage-grass, was found. These depredations make Dipodomys a pest; for though in normal seasons there is enough to go round, in dry years the rodents take a serious proportion, and there is not enough left on the range for stock. Systematic extermination of the little beasts has led to a marked improvement of the grazing and the number of cattle it can carry per acre.

Hundreds of mounds belonging to this animal have been excavated after their inhabitants have been gassed; and in all of them there has been found either a solitary male, a solitary female, or a mother with her family: there are no couples to be found keeping house together. This, it seems, is a further consequence of the sparseness of the vegetation. Each mound is the centre of a largish area from which its owner draws supplies. If two were to live there instead of one, the supply-area would have to be uneconomically large, the animals' journeys in search of food unprofitably long. So the desert has imposed upon our kangaroo-rat this curious semi-bachelor life, in which adults visit each other for sexual intercourse, but never know a family existence.

The same impression of the desert's poverty is brought home by the description of the Tibetan sheep given by a member of the Everest expedition. The tufts of herbage on these high and arid uplands are so few and far between that the sheep can only get enough to survive by running between mouthfuls. They chase their grass.

§ 6

The Tropical Forest

The tropical rain-forest has been the wonder of all naturalists. Alfred Russel Wallace tells us that it was von Humboldt's description of it which lit in him the desire for tropical exploration; but that the reality exceeded his expectations. This rain-forest girdles the tropical lands. It still covers about half of the South American continent—a forest over 2,500 miles from west to east, over 1,500 miles from north to south; man's inroads into its green fastnesses are still negligible; the only way to penetrate it is along its rivers and streams. Africa's forest is equally celebrated; but it is considerably smaller in extent, owing to the height and dryness of much of that continent. And the belt of rain-forest continues round the world, through Ceylon and Malaya and New Guinea.

Naturally there is the greatest variation from place to place; but everywhere this huge expanse of green chlorophyll-machinery, raised high on supporting trunks into the hot, steamy tropical air, has certain features in common. The variations in type occur especially where unfavourable conditions prevent the majority of species from flourishing. In tropical swamps, for instance, the ordinary forest gives place to a theatrical but much more uniform growth of palms; and only mangroves and a few other trees that use their roots as stilts have managed to grow over the mud of tropical estuaries and lagoons.

Under conditions that are altogether favourable for vegetable life the struggle for light is never-ceasing. Here is no dead season when plants shed their leaves and have their roots frozen as they stand. Growth, activity, competition, continue year in year out. The most striking result of this is the huge variety of species that make up the forest. In contrast with the dozen or so kinds of trees in our temperate woods, the Cameroon rain-forest numbers

close on 500. As well as the trees, there are the creepers and the parasites. In this same Cameroon forest, more than 300 species of woody-stemmed plants occur which are incapable of standing on their own trunks but cling to the trees for support. In the great Amazonian forest, these lianas and creepers reach their maximum profusion and their greatest beauty of flower.

Miss Haviland, in her *Forest, Steppe and Tundra*, describes the Amazonian forest as seen from one of its rivers:

> On either side the banks are veiled by a wall of green foliage between one and two hundred feet high, towering above its own inverted image in the water. Here and there its splendid sameness is broken by a patch of coloured blossoms. The branches of the scarlet "rose of the forest" are thrust out over the river, and sprays of Bignonia and other flowering creepers, yellow, purple and red, hang over the trees. The creepers cover the whole roof of the forest as with a canopy, and fall to its foot at the water-side like a curtain. In fact, the forests of the whole Amazonian region may be compared to a series of tables with many legs, separated by waterways and each spread with a cloth which dips to the ground on every side. The table-legs are the upstanding trunks of the trees; the cloths are the tangle of vines and lianas which cover them with a close network. This mass of creepers is not altogether the suffocating burden or host of parasites that it appears to be. In exchange for support, it affords shade which is essential to the well-being of the forest; and it has been shown that when the veil has been torn aside so that the sun can beat down on the roots, the giant trees perish. For this reason an artificial clearing is usually fringed with dead trees.
>
> Here and there dark caverns yawn in the wall of foliage at the water-side. These are the mouths of creeks and streams, shut in by over-arching branches from which long aerial roots hang down like stalactites. To enter these caves by boat is like passing from the open air into a vast dim hall, supported by immense columns. The trunks of the trees rise up for seventy or eighty feet without a branch, and the undergrowth is thin and straggling. The ground is strewn with dead leaves, though it may be remarked that the accumulation of leaf-mould is not very great, owing to the rapidity of bacterial action.

The roof of the forest is the prime source of all its biological wealth, the scene of its greatest activity. As the same authoress says:

In some respects the roof of the forest may be compared with a prairie or savannah. There is the same wide green expanse, strewn with flowers and open to sun and rain and wind. Butterflies hover and grasshoppers skip over the surface, and its denizens are exposed to the unrestricted view of birds of prey—vultures, kites and harpy-eagles—which soar over the forest, ready to seize any bird or monkey which is not alert enough to dive under the foliage.

But, alas! we know tantalizingly little about this zone of brilliant light and rich life. Two-hundred-foot trees are not easy to climb, especially when the attempt brings out armies of stinging bees and biting ants from their nests on every branch. We want a modern St. Simeon Stylites to set up a pillar in the rain-forest and use it not for meditation and prayer, but for the acutest observation and description of the unique life about him. The Oxford Expedition to British Guiana recently accomplished something in this line, but there remains much that is undiscovered. We have already compared the forest to the sea—productive layers atop, with debris of light and food filtering and drifting down. Man on the solid ground of the forest is like a mere flat-fish on the sea-bottom. The tangle of life is layered according to its distance from the roof: in von Humboldt's words, "Forest is piled upon forest."

Those who come fresh to the rain-forest are generally disappointed at first by the apparent paucity of animal life. This is partly because it is dwarfed by the fantastic luxuriance of the plants, partly because the greatest abundance, activity and brilliance of rain-forest animals are up in or near the tops. In the upper zones of the Amazonian forest, for instance, there are squirrels and sloths, tree-porcupines and tree-anteaters, bands of monkeys making the forest resound with their howling, tree-raccoons, climbing cats; there are innumerable birds—toucans, parrots, parrakeets, cotingas, barbets, frog-mouths, forest pigeons and nightjars, curassows, bell-birds. There are the marvellous tree-frogs and tree-toads, many of which never descend to earth but brood their eggs in pouches on their backs, or deposit them in

foamy masses on the high leaves, to go through the tadpole stage in this pretence of a pond; while others put the egg-masses on leaves above pools, whence the tadpoles, emerging slip into the water below. And there are the incredible hordes of insects—tree-nesting ants, and bees, and wasps, and termites; huge butterflies that never come down to ground-level, beetles and crickets and cicadas and plant-bugs that the human collector never sees unless a tree is felled.

What are the chief adaptations in this dense envelope of life? Luxuriance of growth is the first: no tree will ever succeed whose seedlings cannot shoulder their way up to the never-broken green canopy above. The next most striking fact is the abundance of plants that support themselves on others' shoulders in the race for light. Every observer of the tropical forest has commented on the extraordinary way in which the trees are beset with woody cables, thick and thin, like ropes and cordage carelessly and meaninglessly spread among a forest of masts. These are the lianas. Often their stems coil round each other like the strands of a cable, or are provided with a flattened spiral wing. They corkscrew it over the ground, swing in low curves, hang plumb from the upper branches of the tree to which they cling. Here they make festoons of green, there hang in thick curtains or spread as sloping carpets.

Almost all of them have relatively huge conducting pipes to speed water and its dissolved salts up the long thin stem to the leaves. But their actual methods of climbing are very various. Some insinuate their growing tip through the interstices of bushes and branches, later weaving themselves firmly into place by sending out side-branches. The most wonderful of these are the Rotang palms, which have an additional support in the shape of wicked thorns on outgrowths from the tips of the leaves. Up in the light on the roof of the forest world, these thorny anchors wave round in empty air; but the old leaves die, and then the smooth stem slips until the young growth engages with

the tops of the trees. In this way the old stem is continuously being paid out downwards on to the ground, and the total length of stem produced by one plant may reach the prodigious figure of 300 yards.

Then there are the lattice-formers, that make a living trellis from branch to branch of their support; and the twiners, which climb by thrusting their stem spirally round the support. There are the tendril-bearers, which hook on by prehensile tendrils; and the root-climbers, whose stems produce clasping or adhesive roots wherever they come in contact with the support. A number of tropical species of fig have this form of climbing-iron well developed. In addition, many of them, once they have established themselves, let down long aerial roots which penetrate the soil and begin absorption. As a result, the supporting tree is often killed; but the climber, now strong enough to stand on its own legs, remains erect and independent.

Aerial roots are another striking fact of the tropical forest: and many of them are permanently aerial, never striking earth, but hanging like so many bell-ropes in the green gloom. They are the hall-mark of another set of plants that exploit the strength of trees—the so-called *epiphytes*. These are plants which do not even take the trouble to climb, but settle aloft as spore or seed, and begin their growth far above the soil. The aerial roots tap the water in the air, catching the rain before it reaches the ground, drinking in dew, or even sucking moisture from fog or direct from damp air. In this they are aided by an outer layer that greedily imbibes water. Their main difficulty is their supply of mineral salts. Some are dependent on the precarious supplies washed down in the debris of the stems on which they sit; but others have evolved remarkable adaptations for collecting little private gardens of soil up aloft. Some do this by producing a network of roots which grow upwards, nest-like, from the base of the stem and catch the dead leaves and twigs and other rubbish falling from the tops; some collect their humus in a nest

of leaves into which the roots grow inwards and upwards; Dischidia, a Javan epiphyte, produces a set of pitcher-shaped leaves in which water and debris collect; into each of these leaves a special little root-system grows and absorbs what it needs from the soup therein contained. In certain species of Tillandsia (a genus related to the pineapple, other species of which are familiar in the southern United States as "Spanish Moss") roots have been dispensed with altogether; their leaves are arranged to make water-tight tanks, holding up to half a gallon, and are beset with tiny absorptive hairs that take the place of roots. Some species of Tillandsia can even grow on telephone wires, thus demonstrating that they are not parasitic on their support.

Some of the most beautiful orchids are epiphytes; and so are various figs. A number of these latter are only epiphytes for half their lives, for their aerial roots eventually grow down to the soil; and sometimes, as in the liana-figs we have described, these grow columnar and trunk-like and the plant, after killing its host, becomes an independent tree. This is the history even of the huge banyan-fig.

Besides flowering plants there are abundant epiphytic ferns and club-mosses; and many mosses and fungi, lichens and algæ, have found for themselves a station not too far from the light by adaptations to growing on leaves.

But we must not delay too long over the plants of the rain-forest, though it would be easy to fill a book with their beauties and peculiarities. We must pass to the animals. Among the animals the prevalence of the climbing habit is the first and most obvious feature. The forest is inhospitable to man, man an enemy of the forest. He forgets how much of the earth is still covered with trees, how much more was once under forest, not merely before he came to fell and clear, but in the great stretches of geological time when the moister, more equable climate spread the forest zones over much more of the world's surface. And so he is surprised at the abundance of arboreal animals, the importance of the climbing habit in the evolution

of life. Not only has he himself descended from a tree-living ancestry, but the foot-structure of kangaroos and related marsupials makes it certain that they too were once arboreal, and many authorities believe that the ancestors of one great branch of Dinosaurs passed their apprenticeship in the trees.

Be that as it may, arboreal life is common enough to-day. In the Guiana forest, for instance, more than half the known species of mammals are climbers. It is an interesting fact that in the Amazonian forest, the greatest stretch of tropical forest in the world, more mammals than anywhere else have evolved that fine flower of tree-life, a prehensile tail. Only here do monkeys boast this fifth limb; and the tree porcupines, tree ant-eaters, coatimundis and kinkajous also possess it.

Life is so intense and competitive in the rain-forest that adaptations to escape enemies by utilizing colour and pattern are more numerous than in other habitats. The abundance of protectively coloured insects is astounding; the number of creatures, notably caterpillars and plant-bugs, which have evolved some form of terrifying device to bluff their enemies, is far greater than elsewhere; so is the development of nauseous taste, combined with bright colours to advertise the unpalatability; and the intertropical zone is the chief home of that mimicry of nauseous by other species or by one another which we shall discuss in a later section (p. 173).

Devices for enabling carnivorous creatures to deceive their prey are also much commoner. In the East Indies, to choose but one example, there lives a spider which is coloured black-and-white; after spinning a thick whitish web over part of a leaf, it lies on its back in the centre. In this attitude it looks precisely like a bird's dropping, and the web simulates the liquid draining away from it. Many butterflies have a curious partiality for sipping such excrementitious fluids; and H. O. Forbes actually saw one come down to take a drink, only to be captured by the spider.

§ 7

Regions of Rock, Snow and Ice

At the other extreme from the fantastic luxuriance of the tropical forest come the polar regions and their isolated counterparts, the bits of mountain-chains that protrude above the snow line. At both extremes, the severity of the struggle for existence is at a maximum; but while in the rain-forest it is the struggle between one creature and another which counts, in polar and mountainous regions it is the struggle with the elements. In the one case there is over-abundance of food; in the other, the extremity of scantiness.

The scarcity of food which besets land-animals in the polar regions may be illustrated by an incident which befell the Oxford Expedition to Spitsbergen in 1921. The sledging-party had surmounted the huge ice-fall, nearly 3,000 feet high, of the Nordenskiold Glacier, prior to setting forth across the inland snow plateau. They had collected a number of rock specimens and fossils, and cached them, all nicely labelled, to await their return. When they came back, the specimens were safe; but all the labels had been eaten off by desperately hungry arctic foxes.

That was in summer. In the long night of the polar winter the foxes must be still harder put to it, for all their possible prey has left the country, save only ptarmigan, which live in tunnels excavated in the snow, many feet below the surface, and subsist on the frozen shoots of the plants they find there. Some of the foxes are then forced out by hunger on to the sea-ice, where they play jackal to the polar bear when he kills a seal; others remain and try to catch the buried ptarmigan. The few men who stay in Spitsbergen through the winter help beguile their time in the first twilight of spring by trapping. They set traps baited with ptarmigan-heads. If they see fox-tracks going dead straight across the snow, they know the fox has scented

the trap. One trapper traced such a straight fox-track five miles to a baited trap. What a natural sharpness of nose, sharpened still further by what an extremity of hunger, it must need to smell a bit of dried and frozen bird at five miles !

The two polar regions stand in sharp contrast; the high arctic is mainly sea, the antarctic is centred on a huge and mountainous continent. Accordingly, the antarctic is far more rigorous and barren than the arctic. There are no permanently terrestrial animals whatever on the antarctic continent save a few wingless insects that scavenge round the shores. Its only vertebrate frequenters are the penguins—sea-feeders all—the skua-gulls which batten on them, and the petrels. And there are no flowering plants—only a few patches of mosses and lichens.

Perhaps the most striking of all antarctic creatures is a temporary visitant—the emperor penguin. All penguins must breed where there are no predaceous land-mammals, or they would be exterminated; besides offshore islets and oceanic islands, the shores of the great antarctic continent are available for them, for no four-footed beasts exist there. The emperor penguin is one of these antarctic breeders. It is also the largest species of the group; and the young take so long to grow to full size that if they are to be ready to accompany their parents to the open sea and its rich food supplies in the late summer, they must begin their life in winter. Accordingly, these great birds nest in the total darkness of the antarctic winter, on snow-covered land, with temperatures often falling to 60° or 70° F. below zero. One of the achievements of the *Discovery* expedition was an arduous sledge-journey undertaken to study their breeding habits. The eggs and new-hatched young are protected from the cold by being held between the feet and the belly; and so violent is the birds' incubating urge that they will fight each other for the privilege of brooding young—often injuring and killing the chicks in the process—and will even satisfy their desires by incubating lumps of ice instead of eggs.

Thus the penguins, though slow and awkward on land, nest unmolested on the mammal-free continent of the south. Within the arctic regions, on the other hand, there are to be found musk-oxen and reindeer, the wolf, the lemming, the arctic hare, and some valuable fur-bearing creatures, like arctic fox and ermine. Birds are very abundant round the coasts, but only during the breeding season; very few species (like ptarmigan and snowy owl) live there all the year round. Spiders and mites, mosquitoes, midges and sawflies are to be found, often in comparative plenty, and even a few beetles, moths and butterflies. But the abundance of insect-life, so striking in the tropics, is absent. Insects, like reptiles and amphibians, get progressively less important as the climate grows colder, since their activities fall with the fall of temperature. If there were warm-blooded insects, they might well be as abundant in the arctic as birds; but insects cannot be warm-blooded: the limit of size imposed upon them means that they have, compared with their bulk, too great an area of surface out of which heat can leak away. One of the few attempts at warm-bloodedness is made by humble-bees, whose comparatively large bulk and thick, hairy coat hinder the heat generated in their muscles from escaping. While they are moving, their temperature is several degrees above their surroundings: and this property enables them to penetrate much farther north than the smaller and less hairy hive-bees. The lower southward-facing slopes of the Spitsbergen mountains, only 700 miles from the pole, have a rich carpet of bright flowers during the short summer season; and even in the northernmost regions of Greenland there are great stretches of flattish tundra bare of snow in the summer, with a vegetation capable of supporting a population of shaggy musk-oxen.

There are some interesting adaptations to be found both in arctic plants and in arctic animals. Many of the plants, in response to the fewness or absence of bees, have changed over from reproduction dependent upon insect-fertilization to some other method. Some have become self-fertilizing;

others, though they still produce flowers, never set seed, but rely on some form of sexless reproduction. In response to the shortness of the summer many prepare all they can beforehand, and burst into flower and leaf the moment the sun thaws the snow off them. The same thing happens in Alpine regions. Here, however, Soldanella, the ice-flower, goes one better. Its flower begins to grow while the snow-blanket still lies over it; and the heat generated by the chemical activity of its growth actually helps to melt a tiny chamber over the bud and bring the plant to the air a few days before it could otherwise have escaped.

A very interesting effect of the arctic food-shortage is seen in some of the birds. The skuas, for instance, and probably the snowy owls, do not breed every year. In years of scarcity they make no attempt at nesting; their systems probably respond automatically to low temperature and lack of food, their ductless glands are not set in the direction needed if the ovaries are to pile up yolk in their eggs, and the reproductive impulse is never felt. Similarly, butterflies (like the Copper) which in warmer climates may have several broods in a year, in the high north take two or even three years to grow from egg to adult, the caterpillar hibernating between his summer feeding-periods.

But in the polar regions, arctic and antarctic alike, the great contrast is between land and sea. For if the land is poor in life, the sea is rich. For one thing, polar life, so long as it remain in the water, is not exposed to the extremes which it must suffer if it emerge into air. The sea may freeze over; but there is always water below, and this must be above freezing-point. But there is more than this; the life of open waters is actually more abundant near the poles than in the tropics, largely owing to there being more nitrogen salts available in cold than in hot waters. Diatoms discolour the polar seas for miles. Supported by the diatoms live hordes of crustaceans and other small creatures. It is a strange sight to lean over a ship's side in a Greenland

fjord, with rock and ice all about one on the land, and see a constant procession, perhaps one to every square yard, of black specks of life, each provided with a pair of flapping sea-wings—millions upon millions of the pelagic snails called pteropods.

As result of this richness of the polar plankton, the dominant life of both the polar regions lives either in the water or, at least, upon its products. Prominent among these are the hordes of birds which take advantage of their winged mobility to visit the arctic in summer, take toll of the riches of the sea for themselves and their young, and leave for the south before ice and darkness cover their feeding-grounds.

Of the arctic mammals, aquatic forms are pre-eminent. The walrus browses on the shell-fish which he rakes out of the arctic mud with his pick-like tusks; the seals swarm in both polar zones, and have a great range of habits, from the inoffensive crab-eater seal to the leopard seal, the tiger of the antarctic, which loves a penguin if it can get one. Their swimming powers are wonderful. Where there is a narrow passage into a lagoon, with a strong current through it, there the seals delight to play. They will test their powers against the stream, and dart forward in the face of a current against which a ship's boat with four oarsmen can scarcely make headway. Like land-carnivores, they are alert and intelligent—the real dogs of the sea. In the arctic summer, the seals love to bask contentedly on the slow-drifting ice-floes. When they are busy fishing they have to come up to breathe from time to time; this they generally do at particular holes or cracks in the ice; there the Eskimo hunter waits, harpoon in hand, for their emergence. Seals are the staple food not only of the Eskimo, but of the polar bear, which is amphibious, and divides its time between water (in which it swims excellently) and ice. The land it has almost entirely forsaken.

Seals keep warm by means of the thick layer of blubbery fat which blankets them under their skin. It is noticeable,

by the way, that wherever fat is employed as a heat-retainer as well as a store of food, it is spread uniformly all over the body; this characterizes not only seals, porpoises and whales, but also such creatures as reindeer, bears and many other northern land mammals. But in hot climates, where it is needed only as a reserve of food, and the need of the warm-blooded animal is to lose heat, not to retain it, the fat is stored in local accumulations, leaving most of the body-surface unblanketed, as in the hump of the zebu or camel, or the tails of the fat-tailed sheep, and the still stranger North African desert rats or gerbils whose tails are swollen like policemen's truncheons.

Seals, too, like sea-birds, come inshore to breed. The "rookeries" of some species rival those of the penguins in population and bustle.

Whales do most of their feeding in high latitudes. The inhospitable shores of antarctic islands, such as South Georgia, now hum with activity; and the whaling industry grows rich. The biological basis of this prosperity is the whale's need to keep warm; for this he grows his juicy undergarment, sometimes a foot thick, of blubber; and he comes to the antarctic to do it because of the richness of its waters in plankton. But there is a real danger that intensive fishing may bring whales as near extermination in the southern hemisphere as they have already been brought in the northern. World-regulation of the whale-fishery is the only hope.

The bottom life of polar waters is rich, too. Captain Scott's antarctic expedition secured wonderful hauls of such creatures as sea-urchins, sponges and the queer sea-spiders or pycnogonids—all leg and no body.

Recently Stefansson, the well-known explorer, has sought to persuade us that the arctic is not so bad as it is painted. *The Friendly Arctic* he calls it in the title to his book. He points out that the cold is much more intense in north-eastern Siberia than in the arctic, that the tundra supports a rich vegetation far beyond the arctic circle, that what

with reindeer, musk-oxen and seals, the explorer need never want for fresh meat, and that we may hope to solve the world's meat problem by introducing reindeer into arctic Canada and breeding them there on a scale to fit those vast bare spaces.

There is much truth in this; but it is not all the truth. There are the winters to contend with; months of total darkness, even if enlivened by the displays of the Aurora, are hard to face. And the arctic which he speaks about is only the fringe of the arctic. The high arctic, save where local conditions keep it relatively fertile, is desolate enough. The west coast of Spitsbergen is full of flowers and birds in summer, because the climate is kept mild by the Gulf Stream. But the east coast is exposed to the polar current from the north and is barren and forbidding in the extreme. Then again, though it is true that seals abound all round the shores of the polar sea and for many miles northward, they do not seem to penetrate within several hundred miles of the pole. Our world is capped with a flat expanse of ice, barren of all life of mammal or bird, save rare storm-blown stragglers or the still rarer human explorers. On the other hand, as knowledge of weather conditions grows and aircraft improve in reliability, it is on the cards that this desert may see a busy traffic overhead; for it is by far the shortest route from Europe to Japan, or New York to China.

Over the life of the high mountains, interesting though it is, we cannot stay long. Broadly speaking, it is like that of a mountainous polar land, but without any compensating riches like those provided by the polar sea. Just as all land-life ceases long before the poles are reached, so the tops of the highest mountains are absolutely barren of life, plant or animal alike.

The summit of Mount Everest reaches 29,000 feet. On the Himalayas a few plants grow up to 19,000 feet. Most animals stop where the plants stop; but the climbers on Mount Everest saw the tracks of mountain-sheep at 20,000 feet, of hares and foxes at 21,000 feet, and wolf-tracks at

21,500 feet; a vulture was seen flying at 25,000 feet, and a few choughs visited the camp at 23,500 feet and followed the climbers out of curiosity to 27,000.

At lower levels mountain-life, if not rich, is full of beauty and interest. The low-growing plants, tufted and cushiony, often have flowers of a brilliance denied to those of lower altitudes; and there are grazing animals like the ibex and other mountain-sheep, the mountain-goats and the chamois, all with an astounding agility and sure-footedness; and beautiful beasts of prey like the snow-leopard. The biggest of all flying land-birds are mountain-dwellers—vultures like lammergeier and condor; and there are smaller birds like cliff-swallows and mountain-choughs, and the rock-creepers, that search the faces of cliffs for insects, at each upward jerk displaying a crimson flash of wing-feathers.

Perhaps the most impressive thing about the mountains is that life, the insurgent, with all the pressure of millions of years of over-reproduction behind it, has not been able to scale their tops. The highest spot on the earth's surface is only five and a half miles above sea-level; but life has faded out far below.

§ 8

Island-dwellers

Island life is interesting in several ways. The inhabitants of islands afford a proof of Evolution by resembling those of the nearest mainland; yet the isolation which islands provide has brought new types into existence. But what concerns us here is the peculiar stamp which island-life sets upon many of its creatures.

The most obvious characteristic of island-life is the high percentage of flightless forms to be found among the great winged groups of birds and insects. There is a flightless cormorant on the Galapagos. New Zealand still possesses several flightless birds, such as the kiwi, the owl-parrot,

and two or three rails; but once it also harboured the huge moa, a giant flightless goose, a giant flightless duck, and a flightless hawk, all now extinguished, probably by man. The most celebrated flightless bird of them all, the dodo, was an inhabitant of the oceanic island of Mauritius. Its anatomy shows it to have been a ridiculous and overgrown pigeon which had grown small in wing but large in body. The solitaire of the neighbouring island of Rodriguez was another overgrown flightless pigeon. This creature was not so plump, but had evolved a little way in the ostrich direction. On the same island lived a nearly flightless heron, also now killed off.

Then there are a large number of flightless birds which live on one or other of the South Sea Islands. Many of them are rails, which is natural enough, seeing that an ordinary rail spends most of its life without using its wings at all as it skulks through the marsh herbage. And others are moorhens, which also skulk.

New Zealand, though such a number of its birds have lost the power of flight, is not characterized by a very high proportion of flightless insects. It is only the smaller oceanic islands where these abound. Kerguelen and Crozet Islands, down south towards the Antarctic, between South Africa and Australia, are excellent examples. Of seventeen genera of Crozet insects, fourteen are flightless; of eight species of Kerguelen flies, only one lives up to its name and can fly. Nearer home, in Madeira, nearly half the beetles have lost the power of flight, and the same sort of thing is found in Hawaii, the Falklands, and elsewhere.

The adaptive meaning of the winglessness is clear. The insects of small, isolated spots of land will perish if they are caught on the wing by a wind and blown out to sea. Every mutation favouring shorter wings or a lessened inclination towards flight will benefit its possessors, until finally the race loses the capacity and the instinct of flying. For the larger and more powerful birds, however, with their better sense of vision, this will not be so important, though

it may contribute. What will count with them is the fact that an island lacks predaceous land-animals, especially the active mammals. A rôle is thus vacant, waiting to be filled, in the economy of the place, for which the bird may fit itself if it grow wingless. For by sacrificing its wings it can put more strength into body and legs, as does the kiwi; or can escape from the mechanical limitations to size which flight imposes and grow enormous, like the dodo or solitaire; or it can do both, like the moa.

This lack of predaceous enemies may be revealed in other ways. Since island-birds are not under the necessity of escaping notice by matching their surroundings, there will be little selection against the albino and other colour mutations which in all birds occasionally crop up. And, as a matter of fact, white quails are common in the Azores, and pied blackbirds much less scarce than on the mainland, while pied and albino ravens are more frequent in Ireland and the Faroes than elsewhere; and the same is true of many New Zealand birds. The frequent tameness of the birds of oceanic islands is due to the same lack of enemies.

So it comes about that flightless land-birds are typical of larger islands, but only if these lack mammals; while the percentage of flightless insects goes up with the smallness and the storminess of their island homes, till it reaches its maximum in Kerguelen, where a calm day, or indeed a day without a storm, is a rare exception.

There is one other characteristic of island-faunas. When a small island harbours representatives of some large mammal, these are almost always small. One of the most striking examples is the dwarf elephant which lived in Malta in the Pleistocene; and the islands of the Mediterranean still possess diminutive races of red-deer. Such creatures first inhabited what is now the island when it was still connected with the mainland. As seas encroached the island was cut off, and grew smaller; and as it grew smaller subsistence grew less easy to find, and the less bulky creatures survived where the bigger ones starved. For a similar

reason, it would seem, the reindeer on Spitsbergen are of a semi-dwarf race; but here the difficulty of finding subsistence depends more on the barrenness of their land than on its physical smallness. We can imagine the appalling struggle for existence that goes on as such an island shrinks to nothing and disappears below water. For instance, as the plain between England and the Netherlands became converted into the North Sea, what is now the Dogger Bank remained for long centuries as an island. On this a sample of the late Pleistocene fauna seems to have remained for a time, but the whole menagerie was eventually drowned.

§ 9

Cave-dwellers

Underground, in hidden streams and caverns, there lurks a specialized fauna that recalls in certain ways the inhabitants of the abyss. It is for one thing a parasitic world, bare of green plants, since light, the prime generator of all life, is absent. Cave-dwelling creatures either resort there for shelter and protection, as bats or breeding cormorants or rock-pigeons do, and seek their food outside; or, if they are permanent inhabitants, they live on the scanty scraps brought in by the shelterers and casual visitors, blown or drifted in by air, or floated through by subterranean streams. Among these permanencies there are a few beetles, grasshoppers, centipedes and spiders, but these live mostly near the mouths of caves; the aquatic forms are more interesting, especially the crustaceans, fish and amphibians.

It is a curious fact that no cave-dwellers possess phosphorescent organs. Accordingly none have developed large eyes specially adapted for dim light, like some of the deep-sea dwellers, but a large number have become sightless, often developing long feelers or legs with sensitive hairs to make up for their blindness. Many also have lost their pigments and become white, since in the absence of

searching eyes there is no need for the blacks and invisible reds of the deep sea which enable their wearers to blend with the darkness.

Amphibians which have found a refuge from competition in underground water have had to suppress their adult phase, living all their life as gill-breathers, and have become colourless and blind. The best known of these is the strange Proteus of the great limestone caves of Carniola, white (save for its pink gills), and blind, with tiny, sightless eyes. If when young it is exposed to white light, it develops abundance of dark pigment, and the pigmented skin even covers the eyes; but if it be exposed to red light the skin over the eyes remains transparent, the eyes develop, and the animal can be made to see, though its ancestors have been sightless for thousands of generations.

Another such blind and permanently gilled amphibian is Typhlomolge, which inhabits underground water-courses in Texas and is sometimes hurled surprisingly into the light of day from an artesian well.

In some caves, like the Mammoth Cave of Kentucky, large lakes lie underground; and here cave-fishes are to be found—they, too, exhibiting various stages in loss of colour and degeneration of eyes. And there are blind and pallid cave-crayfish and cave-prawns and well-shrimps, albino cave-snails and milk-white cave-flatworms. In the underground channel which leads off water through the mountain-side from Thirlmere to supply the city of Manchester, numbers of the common green Hydra have established themselves, feeding on the debris brought down by the slow current. But in the darkness the green alga-cells which normally live as partners within the Hydra's body cannot exist, and have died or emigrated, leaving the race of subterranean polyps white and transparent.

The cave-fauna presents some of the perennial problems of Evolution in particularly clear-cut fashion. Are cave-animals blind, for instance, for Lamarckian reasons, because of the accumulation of the direct effects of generations of

darkness, or has the inheritance of acquired characters had nothing to do with the matter? And if the Lamarckian view be ruled out, have they become slowly adapted to cave-life by the selection of smaller-eyed varieties? or was there what is sometimes called pre-adaptation, in that animals which happened to have poor eyes or to be blind, sought the shelter of caves and found there an environment suited to their constitution?

Lamarckian views can be ruled out as improbable on various general grounds; but such examples as that of Proteus are additional evidence against them. If it has taken thousands of generations for the effects of disuse to make the eyes shrink to their present size, how account for the fact that a single lifetime in red light will bring them all the way back to normal? There seems to be no doubt that long-continued disuse often leads to inherited degeneration; but the Darwinian would assume that, since selection no longer operates to keep the eyes up to the mark, animals with any mutation leading to incomplete eye-development could survive as well as those with normal eyes, and would, indeed, be at a slight advantage, since there would be less material and energy of growth employed in building up an organ that no longer had any value. There exist cave-animals which would help us to test the rival views. In the old mines of Clausthal in the Hartz, abandoned now for centuries, varieties of water-shrimps and water-slaters (Gammarus and Asellus) occur, almost indistinguishable from the common forms of the illuminated world above, save in their lack of pigment and their half-degenerated eyes. If these were crossed with normal types, and it was found that the difference was inherited in Mendelian fashion, we could be reasonably sure that the degenerate eyes owed their existence to mutation.

There remains the possibility of pre-adaptation. It seems clear that this alone will not account for the blindness of cave forms. For one thing, some cave-animals are found without even a vestige of eyes, even in the embryo, although no such

eyeless varieties have been found in their above-ground relatives. For another, all the evidence at our command indicates that eye-degeneration is a slow process, taking place step by step. This is well shown by the progressive reduction of eyes seen in various related species of cave-fish. Pre-adaptation, however, might play a part in starting a species of cave-life. Creatures that shun the light and do not rely much upon their eyes are much more likely to take to caverns to live in than are light-living species with good vision. But once established in their new habitat, further evolution will be needed to put the full cave-stamp upon them. This process we may call post-adaptation. On the whole (and this question of adaptation to cave-life is obviously only a corner of a more general problem), our knowledge indicates that pre-adaptation, though usually slight, may often be decisive in fixing an organism in a particular environment, while post-adaptation is the more important in working up the detailed correspondences between constitution and surroundings that are so striking to the naturalist in the field.

So far we have dealt only with permanent cave-dwellers; the part-time cave-inhabitants are often of the greatest interest. Bats, for instance, may hang in incredible numbers from the roofs of some caves, and their droppings may accumulate like those of sea-birds to make valuable deposits of guano. But we have no space to enter into the biology of bats, and will conclude this section with a single remarkable example from the Antipodes.

In the Waitomo caves in New Zealand, there are underground lakes whose roofs are studded with tiny points of emerald light. These stars are lights made by insect larvæ—the caterpillars of the fly *Arachnocampa*. Each spins for itself a number of glutinous threads which it lets down from the roof. Whenever any flying creature, attracted by the light, is caught on a thread, the grub above wriggles along and eats its catch. The caves communicate readily with the outer world, so providing abundant prey. When the grubs

are full-fed, they metamorphose, and fly out of the caves to the world outside. Another species is found in Australia; both kinds may live in dark crevices in shady moist spots as well as in caves. A strange feature of the larvæ is their sensitiveness to sound: even voices above a whisper cause all the lights to be extinguished. So abundant are these creatures in some of the caves that they make a subterranean Milky Way whose light is strong enough to see by.

§ 10

Out-of-the-way Modes of Life

Perhaps the most severe conditions which life has to endure, more severe even than the barren darkness of caves, are to be found in hot springs, for protoplasm simply coagulates like white of egg when heated above a certain point. The common grass-frog stiffens and dies thus at temperatures well below that of the human body; and there are very few animals or plants of normal habitats, even in the tropics, whose tissues can stand a temperature of over 40° C. Yet all but the hottest springs have some life in them.

Interestingly enough, the tolerance of heat goes down as we rise in the organic scale. For many-celled animals 45° C. (113° F.) is about the limit; and there are no vertebrates that can stand this, but only a few snails, beetles, worms, and crustacea, while some wheel-animalcules may tolerate a little more. Some single-celled animals on the other hand can stand up to 55° C.: and there are primitive algæ that live in water at 80° C. (175° F.)—nearly hot enough to make coffee with!

These creatures are interesting from the point of view of evolution; for their heat-resisting capacities lie well above anything to be found in more normal habitats; the adaptation to this hot-bath life must therefore be a new and special acquisition, brought about by selection acting on rare and lucky variations.

The same transgression of life's normal power is seen in the inhabitants of salt-lakes and lime-pans. Nowhere else has life ever encountered a salt-content greater than about forty parts per thousand by weight, a figure which obtains to-day in the surface waters of the Red Sea. But in the waters of the Dead Sea and the Great Salt Lake the salt-content is over 200 parts per thousand, and even this concentration is exceeded by certain other salt lakes.

The Dead Sea contains no life; but in the Great Salt Lake there is a typical set of salt-tolerant creatures—a few algæ, the grubs of the salt-fly Ephydra, a water-boatman, the brine-shrimp Artemia, and various protozoa. The brine-shrimp and the salt-fly are the only two many-celled animals that are really successful exploiters of these highly salty waters. The brine-shrimps are sometimes so abundant that they colour the water red, and round some of the Californian salt-marshes there is in summer a black rim, visible from several miles away, consisting of millions upon millions of the little salt-flies that have been produced by the grubs in the brine.

Here again these abnormal powers of resistance must be the result of a special evolution; but the rarity of salt-specialized creatures shows how few must be the mutations out of which such almost unnatural tolerance can be built. The salt-fly grubs are by nature altogether tough. They can live half an hour in absolute alcohol, which will kill most creatures in a second or two, and in four per cent. formaldehyde, a standard killing and pickling fluid for animals, they live over twenty minutes.

Perhaps the strangest abode of life is petroleum. There is a fly called Psilopa which is adapted to live in heavy oil, and is found in the oil-fields of California. And recently oil from a well nearly 4,000 feet deep has been found to harbour a new species of bacterium.

Transitory pools are another queer habitat. The beautiful fairy shrimp, Chirocephalus, may be found living and breeding in the water of cart-ruts. When the water dries

up, it dies; but leaves its drought-resisting eggs behind to be blown away and perhaps to colonize some other cart-rut in the future.

In deserts and semi-deserts, the transitory pools of water brought into being by the rains are almost at once filled with the life that has hatched out of waiting eggs and cysts; sometimes amphibians manage to carry on their species in such districts by laying in the pools as soon as formed, the eggs and tadpoles hurrying desperately through their aquatic life to turn into frogs before the pools disappear.

Aquatic life too manages to exist in tiny hollows in tree-trunks, and even in the moisture absorbed by cushions of moss from showers of rain. In this latter case the drying-out of the microscopic swamps may be a matter of hours instead of days or weeks, and it will not be enough for the animals that live there to possess drought-resistant eggs, since their home will often dry up before even a microscopic creature has had time to get through its life-history: they must be able to become drought-resistant even when adult. The importance of the time-factor in animal affairs could not be better illustrated.

The chief inhabitants of these tiny moss-marshes are bear-animalcules (which mostly suck the juices out of the moss-cells, and cling on with hooked claws to prevent themselves being swept away by rain), small round-worms, wheel-animalcules and a few tiny crustacea; and they can all, at any time of their life-history, respond to drought by shrivelling up and banking the fire of their life so that it merely smoulders; in this state they can wait for months or even years until moisture again swells them to sappiness and activity. The seasons do not exist for these creatures; every now and then their existence is broken into by periods of suspended animation, out of which they emerge to take up their life at the point where it was interrupted.

The nests of ants and termites have their own highly specialized group of inhabitants; but of them we have no space to tell here. Even dung may provide a definite habitat:

a distinct and specialized fauna and flora lives in and under cow-droppings, for instance. And there are a host of queer habitats provided directly or indirectly by man. Not only is there a rich fauna on sewage-farms, but a study of its habits is proving vital to scientific sewage disposal; and the inhabitants of waterworks are equally interesting and important. Sand-filters are widely employed in modern water-supplies; they are of the greatest value, since they will prevent the passage even of bacteria. But this is not due to the mechanical filtering power of the sand, but to the much finer filter formed on its surface by microscopic plants, mostly diatoms. This guards our water-pipes against two dangers—first against bacteria dangerous to health, and secondly, against invasion by the eggs and other reproductive bodies of animals and plants which might then sprout and grow there.

When the water is not filtered, surprising results follow. Hamburg in 1886 was supplied with water from the Elbe, unfiltered, and stored in reservoirs for a quite inadequate length of time. Fresh-water shrimps began to pop out of the taps, and the pipes to get blocked with growths of Polyzoa, and even occasional eels. In 1886, Professor Kraepelin, by means of a wire-gauze cage which could be screwed on to the mains as desired, investigated the fauna of the water-pipes. The smallest creatures, such as Rotifers, passed through the meshes of the cage; but even so he secured specimens of fifty different genera of animals. Sponges encrusted the pipes, with huge mossy growths of Polyzoa and hydroid polyps, which often came away in tangled masses. There were plenty of worms, segmented, flat, and round, and of bivalve molluscs; shrimps and other crustacea, both fresh-water and marine, were not uncommon, notably "loathsome swarms" of the common water-slater, Asellus. Once a small flounder was captured; there were a fair number of sticklebacks; and eels (up to a foot in length) infested the pipes in thousands. In spite of the revelation of this huge fauna under the city streets, nothing

was done for years. The population was easy-going, and the manufacturers of domestic filters, who did a roaring trade, succeeded in putting off reform. Then one day came the crash; in 1892 the waters of the Elbe became infected with cholera germs, and over eight thousand of the people of Hamburg died of that dread disease. Sand-filters were installed; the mixed fauna was barred from the biological Eldorado it had found in the pipes; and the people of Hamburg no longer ran the risk of cholera.

But we must bring our chapter to a close, although the catalogue of strange lives could be continued almost indefinitely. Let Mr. Everyman stroll round his garden and look (to give him a few suggestions) under stones, among dead leaves, on the branches of living trees, in the rain-butt, on the mouldering wood of an old fence, to see how many different habitats, each with its own peculiar zoo, he can find.

CHAPTER IV

SOME SPECIAL ASPECTS OF LIFE

§ 1. Partnership and Parasitism.
§ 2. The Scale of Living Things.
§ 3. Colour and Pattern in Life

§ 1

Partnership and Parasitism

IN the previous chapters we have tried to show how life presses and crowds into every nook and corner of the earth's surface that is habitable. We have found life exuberant and various in hot springs, deep caves and dunghills, on remote oceanic islands, on frowning mountain crags; in all these places the same drama of hopeful germination and bitter struggle. But we have said little so far of how life jostles life, how, in virtue of that same life-pressure which injects organisms into the tiniest cracks on our world, living things impinge on each other. And yet a large part of the effective environment of any given kind of animal or plant consists of other animals and plants. The struggle for existence forces them into mutual relationships, often of the most intimate and extraordinary kind. In this section we shall describe some of the most striking of these, and show how, as in the more plastic changes of human relationships, casual association may pass over into mutually helpful partnership, or the undercurrent of competition may transform partnership into parasitism; how no sharp line is to be drawn between parasitism and the straightforward

relation between devourer and devoured; and how difficult it may be to distinguish between service and slavery.

Of the larger animals and plants, perhaps the majority live in intimate association with humbler organisms. Our own mouth-cavity and intestines harbour millions of bacteria, spirochætes and protozoa. Most of these are neither harmful nor the reverse to their giant host; they simply take advantage of the peaceful warmth and food provided by his tubular interior. But in herbivorous mammals the bacterial flora is part of the machine. Without bacteria, the mechanism of a horse would not work; for it is they which act as chemical tin-openers to all those microscopic boxes, the plant-cells, in which the digestible part of his food is locked up. To such mutual arrangements by which both partners gain there is generally given the name of *symbiosis*—a joint life. And then there are bacteria, no different in general appearance from any other sort, which penetrate into blood or tissues and there grow and multiply at their host's expense; they are parasites.

The abundance of parasites is extraordinary. Most species of animals harbour several different kinds of parasites, and though most of these are common to several hosts, the total number of parasite species must be almost as great as the total number of free-living creatures. There are plenty of examples—the tape-worm, with its never-ceasing production of jointed living ribbon, each segment, when mature, being impregnated by one of its neighbours, and later dropping off to disseminate the embryos with which it is packed for the invasion of a second host; the liver-fluke with its cycle, now in sheep and now in snail, always changing its form, but always a destroyer; Sacculina, ramifying through the whole organism of some unfortunate crab, eventually bursting out like a hernia before killing its host, a bulging bagful of sperm and eggs; the guinea-worm, a living thread up to six feet long, making abscesses in human flesh through which to discharge its eggs, hardly to be got rid of save by winding it out, perhaps an inch a

day, on a slip of wood which between whiles is fastened to the limb; the dreaded Trichina of measly pork; the roundworms of our own and our dog's intestines.

We will describe a few others in more detail. The hook-worm is another roundworm. Its eggs leave human bodies in the fæces; its young stages live free in moist earth, and gain entry to human body again by scratches in the skin. Bare feet and bad sanitation keep it going. Once inside, it is carried by the blood to the lungs, there forces its way into the air-spaces, and then, exploiting for its own use the normal human protective mechanism by which alien particles are expelled, is carried up to the mouth by the beat of the ciliated cells. Then it is swallowed; arrived at the intestine, it bites on to the wall with its powerful jaws, and remains there sucking blood until full-grown. A heavily infected man may contain many hundreds of hook-worms, each about half an inch long, all draining his life-blood. No wonder that the human population of hook-worm areas are anæmic, listless and unprogressive.

Insects, if parasitic, are usually parasitic during their larval stages only. One of the most familiar examples is the ox warble-fly, which ruins thousands of hides every year; the eggs are laid under the skin, and the maggots cause the "warbles"—large swollen lumps—through holes in which the flies eventually emerge. The horse botfly, on the other hand, penetrates farther. The eggs are laid on the limbs; they hatch within a day or so, and the tiny larvæ cause such itching that the horse licks the part and, without knowing it, swallows the maggots. Thus obligingly brought inside, they fix tight on to the stomach lining and grow there for the best part of a year.

Other flies lay their eggs in the noses of men and beasts, and the growth of the maggots may cause much suffering and even death. And there are a number of blowflies which have departed from their normal habit of breeding in decaying flesh to deposit their eggs in open sores on living animals. The maggots live on the decaying flesh,

and their presence ensures a continuance of the food-supply by aggravating and enlarging the wound. There are many millions of sheep in Queensland; and of each million nearly 50,000 die a fly-blown death every year.

A rather different form of parasitism is found in many hymenoptera. Some of these are so small that their grubs are parasitic only on other insects' eggs; but most of them parasitize other grubs. The female ichneumon-fly, by means of her long sharp ovipositor, lays her eggs deep in a caterpillar's body. The young hatch out and devour the animal from within, as if a brood of rats were to eat their way through a living sheep. At first they spare the vital organs, confining themselves to fat-stores, connective tissue and the like; so that their host can still continue to feed and supply them with nourishment. No killing of the goose that lays the golden eggs! But the last golden egg produced for them by the caterpillar is that it should transform itself, when full-grown, into a pupa with a tough protective shell. Once safe within that, the ichneumon larvæ eat all that remains, themselves attain to full growth and bore their way out to pupate.

One does not at first know which to be more impressed by—the admirable delicacy of the adaptation or the refinement of cruel exploitation. Such facts are, indeed, a real difficulty for those who believe in the creation of the world as it stands by a beneficent deity. But they offer no such moral problem to the evolutionist. Natural selection is a blind agency and knows no human values. It is as unjustifiable to ascribe moral qualities, such as cruelty or beneficence, to animals or the processes of their lives, as it is to ascribe purpose to the wind or consciousness to a mountain. The processes of Nature know no values; all values arise in the mind of man.

Microscopic parasites can be equally deadly. Those single-celled flagellates, the Trypanosomes of sleeping-sickness, are even beautiful with their flagellum attached to a transparent fin-membrane, as they undulate their way

through a crowd of blood-corpuscles. But they multiply in the blood and then invade the cerebrospinal fluid; the patient grows drowsy and wastes away, a ghastly bag of skin and bone, to an almost inevitable death. This microscopic flagellate killed over 200,000 men in East Africa in seven years; and a near relative, which causes the nagana disease of domestic animals, makes it impossible to use horses, donkeys, cattle or mules over several million square miles of the same continent.

Animals are not parasitized solely by other animals. The bacteria are the most important of any parasites. They are all commonplace in appearance; their virulence is chemical. The bacillus of plague is a microscopic rodlet like any free-living bacillus; but it kills men like flies. The bacteria are as giants compared with the filter-passing viruses. But size is no criterion of deadliness; such virulent diseases as yellow fever and smallpox and foot-and-mouth are the result of parasites so small as to be ultra-microscopic.

Plants too may be parasitic. The spores of the fungus Cordiceps invade the tissues of caterpillars; then they germinate into a mass of filaments, which eventually permeate the host. Finally, the caterpillar creeps down to the ground and dies, while the fungus sends out its fructification in the form of a long horn-like structure from the host's head. The caterpillar may be almost wholly vegetalized in death, and remain converted into a woody mummy for several months. Ringworm is due to another fungus which flourishes on living human skin.

Then there are animals which exploit plants. The most striking cases are those of the gall-producing insects and mites, the most abundant being midges and tiny hymenopterans. Their strange power it is to make their plant-host produce both food and shelter for their young. They lay their eggs on leaves or flowers, stems or roots; and the plant-tissues grow up round the developing grub to make a gall—a structure often quite unlike anything normally

produced by the plant. The round fleshy oak-apples on oak leaves and the brilliant red feathery robin's pincushions on roses are familiar examples. Sometimes the gall's structure is eminently adaptive—for the needs of the parasite; on sweet-gum trees you may find galls consisting of a central chamber lodging the grub, connected by a system of radiating struts with a protective shell outside.

It is not known how the insect forces these wonderful transformations on the plant-tissues, whether by substances injected with the egg or by some stimulus emanating from the grub. If we could but discover their secret, we should be another big step forward towards the control of growth-processes.

And plants may parasitize plants. One of the most interesting as well as economically important of plant parasites is the fungus known as rust of wheat. We will speak of some of the rusts in a later chapter. A strange case is that of the flowering plant Rafflesia, a native of Malaya. This lives the whole of its growth-period within another plant. It has lost every vegetative organ which its ancestors possessed. Its host provides roots and root-hairs for anchorage and for sucking water and salts from the soil, leaves and chlorophyll for tapping carbon from the air, bark for protection, wood for support, and all the microscopic pipes for transportation; and so Rafflesia has need of none of these things and has come to consist merely of a tangled web of white filaments, very like those of most fungi, penetrating the host in every direction. All it has to do is to provide an absorptive surface; its host does the rest. However, the host-plant cannot very well provide for its parasite's reproduction; and so when the time comes, this degenerate mass of microscopic fibres gathers itself together here and there, breaks out to the exterior, and there grows out into blooms as elaborate and finished as those of any self-supporting plant. Indeed, in one respect they outdo all others: for *Rafflesia arnoldii* from Sumatra holds the world's record for flower-size, its blossoms some-

times exceeding a yard in diameter and weighing up to twenty-five pounds apiece.

This is a close parallel with the animal parasite Sacculina, which at an early stage of its career is altogether inside its host, and consists wholly of a network of absorbing rootlets; and only later, for the purpose of reproduction, bursts through to the exterior and organizes a body with a definite anatomy.

It is worth emphasizing that parasitism and independence grade imperceptibly into each other. In the matter of food all animals are exploiters, either of other animals or of plants. Usually, however, the exploitation involves an elaboration of structure rather than a degeneration: one need but think of carnivore lion or herbivore horse or the beautiful sifting machinery of mussel or oyster. Some small caterpillars eat their way through the interior of fruits or stems or leaves. We do not generally consider them parasites for that: they are internal herbivores. But internal carnivores also exist, and in all degrees. Lampreys bore holes into the living bodies of their victims, and their relatives the hagfish may eat their way right inside. Miss Worthington writes that on the Pacific coast of America many of the fish caught on night-lines are found to "have been entirely eaten away, nothing but the skin and bones being left. The hag-fish has bored inside the skin and eaten all the soft parts, and is sometimes caught in the very act of wriggling away at the close of its meal." Up to three or four may be found eating out a single fish. Such animals penetrate their victims only temporarily, but from this condition to the continuous internal carnivorousness of ichneumon-grubs is not a large step.

Among green plants, the same sort of series may be traced. Even within a single tribe of the family Scrophulariaceæ all gradations from independence to obligatory and complete parasitism occur. Many of them are always respectable green plants, independently manufacturing their nourishment out of air, water and soil-salts. The yellow

rattles (Rhinanthus) have their feet on the first rung of the descending ladder: they *can* grow and reproduce in independence, but they often tap the roots of other plants with their own; and the pretty little eye-bright, Euphrasia, which no one would take for a subterranean vampire, behaves in the same way. The cow-wheats (Melampyrum), on the other hand, though they can germinate in isolation, die later unless they can parasitize their neighbours. Special side-roots are developed which, if they touch the root of another plant, grow round it, penetrate it here and there, and establish direct connection between their own water-conducting tissue and that of their host. By this means a single plant of cow-wheat may simultaneously tap the roots of several hosts belonging to different species.

Even here, however, the parasitism, though obligatory, is only partial, since the plants still possess green leaves and manufacture their own carbohydrates. The mistletoe is in a similar category. The mountain plant Tozzia is a rung lower. It germinates below-ground and for several years lives as a mere subterranean stem, entirely parasitic on other plants. Then it sends up a flowering shoot with pale-green leaves, poor in chlorophyll but still capable of making some contribution to its nourishment, and lives the brief rest of its life as a partial parasite. Finally, in the toothworts parasitism has become complete. They never produce any chlorophyll at all; they draw nourishment from other plants all their life long, penetrating right to the woody pipes of their hosts with special sucker-organs; and their seeds seem incapable even of germinating unless they happen to lie against the right kind of root. The broomrapes have independently evolved into equally complete parasites.

These are all one-sided arrangements. Now take the opposite category, true partnership or symbiosis, in which the partners benefit mutually from their association. In the most extreme cases neither can exist without the other. Perhaps the most remarkable of these is the partnership

between fungus and alga which has given the world the whole new group of compound organisms, the lichens, and enabled plants to push farther into the barren places of the earth than they could ever have done otherwise. The most important of such partnerships to us is that between leguminous plants and certain kinds of bacteria. Already in Roman times legumes like lupin and vetch were grown to enrich exhausted soils. We know now why the soil is thus enriched. If you pull up a plant of this sort, you find irregular swellings on its roots; and these swellings are inhabited by countless millions of bacteria. These bacteria have the power, denied to higher plants, of seizing and using free nitrogen from the air. They can do this to a limited extent when living on their own in the soil. But their nitrogen-fixing capacity is enormously multiplied when they are living with their big leguminous allies. These supply an abundance of carbohydrate materials; the bacteria obtain energy by breaking these down to simpler substances, and use this energy to conquer the chemical inertness of the atmospheric nitrogen. The green plant is good at fixing carbon, the bacterium at fixing nitrogen; in the partnership the two advantages are pooled.

Knowledge of these facts is of considerable practical importance. To get lupins or lucerne to grow well on new soil, poor in nitrogen bacteria, either they or the soil must be inoculated with the bacteria. Large areas of barren sandy lands in East Prussia have thus been reclaimed through lupins; and a new method of inoculating lucerne with its microscopic partner is now proving of great value in extending the area of that useful forage crop through various regions of Britain where it was hitherto not grown.

Another important symbiosis is that between termites, the so-called "white ants" of warm countries, and the bizarre microscopic flagellates which crowd their intestines. The flagellates can do what the termites, like ourselves, are helpless to achieve—they can break down cellulose and even wood into digestible substances. By exposing the

termites to high temperature and by other methods, such as treatment with oxygen under pressure, the protozoa can be killed without damaging their partners. But termites thus deprived of their internal flocks and herds are powerless to digest their ordinary diet: abundant wood is now as useless to them as a bare table would be to us, and, although they go on eating, the chewed wood is passed out unchanged and they perish of starvation.

The termite with its powerful jaws provides the raw food-material for the joint household partnership, and also the protected kitchen for its due preparation. The flagellates alone can achieve the culinary transformations there, and digest for both. As a result, the termite-flagellate partnership is the great scavenger of the tropics, before whose attacks leaves, twigs and the fallen trunks of great forest trees melt and are destroyed, and their substance brought back into the vital circulation far quicker than by the ordinary processes of slow decay. As further result, however, white ants are among the most inveterate destroyers of houses and furniture, books and papers, in low latitudes. If the alga-fungus partnership has extended the range of humble plant-life in the arctic, that of termite and flagellate is hindering the spread of human civilization in the tropics.

Then a great many animals are green, owing to the presence of single-celled green algæ within their tissues. Among these are many of the beautiful Radiolaria that float in the sea, the green Hydra, and the great majority of reef-forming corals. The animal profits by utilizing some of the carbohydrates built up by the alga's chlorophyll, and therefore need not trouble to find so much food; and the alga profits by utilizing some of the nitrogen which the animal is continuously giving off in its excretions, for there is in most habitats a shortage of available nitrogen, and an alga within an animal finds itself in an exceptionally favourable situation as regards this element. We have seen that the chief reason why reef-building corals cannot live save in a narrow surface layer of water is that they

starve at greater depth, since their algal partners need light to make their carbohydrate contribution to the partnership.

During the last fifteen years, Buchner has been making a systematic study of symbiosis between animals and plants, and has discovered many interesting facts. Partnerships between animals and green algæ are confined (with the one exception of the sloths) to transparent and water-living creatures, for only here can the food-producing activities of the green cells be turned to advantage. We find them in protozoa, sponges, corals, and other cœlenterates, flatworms, wheel-animalcules and possibly in a few pelagic snails.

When the plant-partners are algæ, they help in food-manufacture; when they are fungi or bacteria, they help in food-utilization. All arthropods that suck plant juices have such partners—plant-lice, scale-insects, plant-bugs, cicadas and the rest. So do all those that suck the blood of vertebrates—lice, bed-bugs, ticks, mites, tsetse-flies, probably mosquitoes and fleas, with leeches too; but their relatives that suck invertebrate blood have none; apparently the colourless plant-partners help in breaking down that typical vertebrate structure, the red blood-corpuscle.

Hair- and horn-eaters like the bird-lice are also dependent upon symbiotic partners; and so are all the wood-eating animals and those whose diet is very rich in cellulose. Many beetles and beetle-larvæ, termites (though here the partner is a protozoan), ants, wood-wasps and gall-midges, ruminant and rodent mammals, and certain birds all fall into this category. Here, the partner-plants help to make an unusual type of food digestible. Where animal food is the staple, we find no bacterial or fungal partners. All cockroaches too are really partnerships, though in this case we do not know exactly what rôle the intestinal bacteria play. In some cases, bacterial partners appear to supply certain vitamins to animals living on a monotonous and qualitatively deficient diet.

Finally, partner-bacteria may play quite a different rôle—they may be used to generate phosphorescence. Many

animals shine with their own light, but there are a number —most of the luminous cuttle-fish, all the brilliant Salps and Pyrosomes among the sea-squirts, and a few fishes— which cultivate luminous bacteria in special pockets evolved for the purpose. Symbiosis is thus not a haphazard occurrence. It has its rules and its meaning; each kind of partnership between an animal and a plant is helpful in a particular way of life.

A partnership less essential and less intimate, although no less interesting, is that between a common species of hermit-crab, *Eupagurus bernhardi*, and a sea-anemone. The mollusc-shell inhabited by the crab is always covered by a pink sea-anemone of the genus Adamsia. When the crab has grown too big for its house, and must change into another, it carefully detaches its partner and fixes it on the new shell. The hermit-crab with very little trouble and expense obtains a defence-force in the shape of the anemone's white stinging thread or acontia, covered with batteries of poisonous nettle-cells, which it shoots out when alarmed through little port-holes provided for the purpose in its flanks. The anemone gains transport and crumbs from the crab's table, as its active jaws break up a piece of carrion. The anemone's sole adaptation to a life of partnership seems to be its readiness to be detached by the crab, whereas to any other detaching force it offers the greatest resistance. Other crabs live with evil-tasting sponges; or carry sea-anemones in their claws as living knuckle-dusters.

From such examples one would imagine that symbiosis and parasitism were clear-cut biological categories. But consider a few others.

The common ling, or Scotch heather, *Calluna vulgaris*, is one of those numerous plants which have entered into partnership with a fungus. It is a real dual organism, like a lichen; the fungus extends its web of filaments right through the plant, most abundant in the cells of the roots, but reaching through stem and leaves and even into the ovaries. As the seed ripens, filaments extend on to its

coat; and when it is shed and begins to sprout, these penetrate the living cells of the root. They secrete a ferment which dissolves cellulose; and by means of this, the filament spreads from cell to cell. After a short time nearly every cell of the root's outer layers contains a coil of this microscopic living threads; and thence it spreads up the stem. Finally, it bursts out on to the outside of the root, there to form a microscopic feltwork, and also, though in less quantity, on to the outside of the leaves. So far this looks like a case of parasitism. But, surprisingly enough, it has been proved that the fungus feltwork round the roots is necessary for the life of the ling. If heather seeds are sterilized, so as to rid them of all traces of the fungus, and then sown, they begin to germinate; but, though stem and a few leaves at first grow normally, nothing of the root-system is formed save a few feeble stumps, and the rootless seedlings soon die. The fungus, on the other hand, can grow apart from its larger partner, and when thus isolated, it has been proved to have the power of fixing nitrogen from the air. Moreover, it has been shown by Rayner that the heather-fungus partnership—in other words, fungus-infected seeds—could germinate and grow quite well in spite of the absence of all nitrogen supplies, organic or inorganic, showing that the fungus was obtaining the necessary supplies of nitrogen from the atmosphere while in double harness just as well as when on its own.

Here, one might now suppose, is a perfect case of mutual benefit. The fungus receives carbohydrates made by the chlorophyll-machinery of the heather, the heather appropriates some of the nitrogen made available by the peculiar and specialized chemical activity of the fungus; and so long and close has been the partnership that the heather is now entirely dependent upon the fungus, and even needs its presence as a formative stimulus to its normal development.

But it is only in certain conditions that the partnership works thus smoothly and with mutual benefit. We have seen that heather seedlings grown without any fungus will

come to nothing. But even if they are inoculated with some of the fungus, the partnership is only successful when they are supplied with little or no nitrogen salts. If more nitrogen is provided, the fungus grows too vigorously. It takes the upper hand, becomes a parasite instead of a partner, and kills the heather seedling. Through some subtle chemistry we do not yet understand, the balance is tilted, the regime of mutual help is destroyed and gives place to a regime of exploitation. Ling will only grow in certain kinds of soil. Possibly this is due in part to similar upsets of the unstable partnership.

Nothing could better illustrate the precariousness of life's adjustments. The phrase "hostile symbiosis" has been used to describe the state of our own tissues—all of the same parentage, all thriving best when working for the common good, and yet each ready to take advantage of the rest, should opportunity offer. There is a profound truth embodied in the phrase. Every symbiosis is in its degree underlain by hostility, and only by proper regulation and often elaborate adjustment can the state of mutual benefit be maintained. Even in human affairs, partnerships for mutual benefit are not so easily kept up, in spite of men being endowed with intelligence and so being able to grasp the meaning of such a relation. But in lower organisms, there is no such comprehension to help keep the relationship going. Mutual partnerships are adaptations as blindly entered into and as unconsciously brought about as any others. They work by virtue of complicated physical and chemical adjustments between the two partners and between the whole partnership and its environment; alter the adjustment, and the partnership may dissolve as blindly and automatically as it was entered into.

In Calluna, beneficial symbiosis may pass over to true parasitism. Other partnerships partake of both qualities simultaneously. Take for example the little flatworm *Convoluta roscoffensis*, whose partnership with a single-celled green alga has been so graphically described by Keeble in

his *Plant-Animals*. This all but microscopic worm-alga partnership is so abundant in some regions, as at Roscoff in Brittany, that it colours the sand green over patches many yards in extent, its hordes coming up with the inflowing of the tide and burrowing below the surface, out of reach of the pounding waves, as the beach is covered. Over 2,000 million wormlets may exist in each square yard of such a patch. Convoluta, unlike the heather and the fungi of the most specialized kinds of lichen, does not take steps to carry over a supply of its microscopic partner in reproduction; its eggs are colourless, free of algæ. But the algal partner is abundant as a free-living creature in the environments where Convoluta is found; and every egg is soon surrounded by a little band of these green flagellates, attracted in all probability by the nitrogenous substances it gives off as waste. The egg develops into a larva, which one day swallows one or two of the green free-living cells. These multiply in its body and produce the large quantity of green tissue. A worm kept uninfected in sterile water not only remains colourless but fails to grow and after a short time dies.

The adult Convoluta thus contains a whole band of algæ. These find themselves in a very favourable situation for growth, since they snap up the animal's waste nitrogen before it diffuses out into the sea; and Convoluta, by its periodic migration to the surface, puts the algæ into the best conditions of light for splitting carbon dioxide. The worm, on the other hand, draws on its partners for food. While it is growing, it still eats in normal animal fashion, but once it is full-grown, it no longer uses its mouth, but nourishes itself entirely by digesting away the surplus of its green cells. So we have the strange spectacle of a worm that grows vegetables within its own flesh.

As the worms grow old, they mate and lay eggs. Then somehow the balance is upset and the whole internal population of algæ is digested; and when this has been accomplished, the Convoluta must die of starvation, since it is

incapable of finding food for itself. Every worm of these millions on the beach, if it escapes a more violent end, is destined to starve, as a result of this incontinence of its own appetite.

During most of each worm's lifetime, the partnership is a symbiosis, for both worm and alga benefit; but in its old age the partnership changes its character and the worm becomes a parasite, or rather a straightforward herbivore, destroys its plant-partners, and with them both the partnership and itself. From the point of view of the race of algæ, the partnership is never a symbiosis, since every alga within the body of the worm is in the long run doomed to destruction; the algæ are lured into slavery by the chemical bait dangled before their nitrogen-hunger, and are cared for only to be destroyed. The relation is like that between man and some animal which he would take into captivity only to fatten and kill, leaving the supply to be renewed by natural reproduction. Some kinds of oyster-culture approach this, although man here usually in some degree controls the reproduction of the subordinate partner; and luckily man is not inexorably tied to dependence upon oysters as Convoluta is to dependence upon its algæ.

Then both symbiosis and parasitism grade off imperceptibly into more casual relationships. The termite and its flagellate are indissolubly tied together—neither can live without the other. Ling cannot live in nature without its fungus; but the fungus can live without the ling. In many lichens both partners can exist separately, but they cannot grow under anything like such a range of conditions as can the partnership of both together. In other cases the relation is less obligatory. Almost all the familiar forest-trees of the temperate zone normally possess fungus in and on their roots like ling; such root-fungus is called mycorrhiza. Often the infected roots are covered with a visible feltwork of fungus, and this growth may be different from the normal. No root-hairs are formed when the mycorrhiza is present, the fungus threads apparently taking their place.

The fungus is found actually inside many of the tree's cells. In some cells it is actively alive and growing; elsewhere it may die, and the tree-cells digest it. There is little doubt that in certain soils the proper development of the tree is bound up with the presence of the right fungus; but in certain conditions the trees can grow independently, without assistance from their fungi. At any rate, they are not, as species, inevitably tied down to the partnership.

The fungus-partners of many forest-trees lead a double life. Like so many fungi, they spend most of their existence as a mycelium, a thready feltwork of tiny white threads, penetrating the rich soil in all directions. If the threads continue their independent life, they eventually throw up a large toadstool to disseminate the race by means of spores. But if they chance to meet a tree-root, they find in it a habitat which is equally propitious but quite different. They change their whole mode of growth. The invasion of the very cells of the root at once suggests that the fungus is a parasite on the tree; but the digestion of a certain proportion of the fungus equally suggests that the tree has lured (metaphorically speaking, be it well understood) the fungus within itself to enslave and exploit it, as Convoluta enslaves and exploits its algæ.

Our simple human categories of exploitation and mutual benefit, although useful, are artificial, and break down when confronted with the complex and inhuman, or at least non-human, realities of other life. Fungus and tree-root penetrate where they can and increase their substance blindly at the expense of whatever material they find; selection sees to it that beneficial variations are appropriated as they turn up. The fungus invades, the root resists; there is a balance between the invasion and the defence; there are some advantages on both sides, but damage on both sides also. The advantages reaped by either of the competitor-partners may cancel out its losses, and the net result be nil; or one may achieve a net benefit and to a certain degree exploit the other; or adjustment may be made so that in both the

benefit outweighs the damage, and thus a true symbiosis arises.

We have seen that parasitism grades into the mutual dependence of symbiosis. It also grades into independence[1] —in animals generally the independence of the carnivore or the scavenger, in plants that of the green plant or the chemically scavenging fungus. It has usually been customary to call any organism a parasite which both lives on or in another and lives at its expense; but by so doing, we lump together a number of really quite distinct ways of life. Whatever our definition of parasitism, it is clear that such forms as a tapeworm, a Sacculina, or a Rafflesia must be called parasites. They not only live at the expense of other organisms, but in so doing have sacrificed their own independence of life and lost the organs by which it was once achieved—the animals their limbs and stomach and sense-organs, the plant its leaves and stem and roots, and even its very greenness.

But what of the bird-lice or Mallophaga, which find shelter under the plumage of birds and only live by scavenging the debris of the feathers? What of the ichneumon-grubs that eat out the inside of their caterpillar-host and could just as well be called internal carnivores as parasites? Is there enough difference between the habits of a flea and a mosquito to justify us in calling one a parasite, the other not? What about the Remora or sucker-fish which obtains free transport from sharks and turtles and other large sea-beasts by clinging to them with the sucker on its head, but takes no food from them; or the gall-forming crab Haplocarcinus, which robs the corals among which it lives of no nourishment, but by the irritation of its presence distorts the growing tip of a coral branch into a bulbous protective case for itself? What of the little crustacean which inhabits the hollow interior of the barrel-shaped Salps, and scoops up its host's food as it is being slowly propelled by cilia along the food-groove

[1] The independence of animals and fungi is a relative independence only; they are in the long run dependent on green plants. See Chap. V.

inside its pharynx? What of the cuckoo, which lives at the expense of other birds when it is young, but then fends for itself?

The truth is that animals or plants can no more live in "splendid isolation" than can nations. Every organism is part of a network of relationships, biologically tied to a host of others. There are relationships concerned with feeding, with shelter and protection, with support, with reproduction, sometimes with such minor matters as toilet and recreation. Within every sort of relationship, one party may not only come to exploit the other, but to exploit it in such a way that it loses some of its own independence and becomes, in the biological sense, degenerate. Or the two parties may come to benefit each other. But all relations of any intimacy, between lower organisms as between men and women, are precarious, supported, as it were, on a knife-edge. They may so readily over-balance and change into something different and even opposite.

§ 2

The Scale of Living Things

In the preceding chapters we have set out something of the diversity of plans of structure and ways of existence. Life's purely quantitative diversity is no less striking.

It may interest the reader if we give a brief scale of sizes. The biggest plants are nearly ten times bigger than the biggest animals. The biggest animals are whales, some of which must run [illegible] and fifty; contrary to popular belief, the biggest extinct reptiles weighed only some fifty tons, or about a third as much as the giants among these biggest mammals. These giant reptiles were undoubtedly semi-aquatic; and water-animals can reach much greater weights than land-animals. Of land-animals, some extinct forms exceeded ten tons, but among those alive to-day, six or seven tons is the maximum.

All these are vertebrates. The biggest invertebrates are molluscs, some of the giant squids reaching two or three tons. The cœlenterates, startlingly enough, come next; a jelly-fish from arctic seas may weigh about half a ton. This group is followed at some distance by the arthropods, with giant spider-crabs of perhaps fifty or sixty pounds. Among groups which exceed two pounds, but fall short of ten, are snails, lamp-shells, echinoderms and also—a surprise to most people—earthworms and polyps. Perhaps, too, the largest tapeworms, with their huge lengths of seventy feet and more, just reach a kilogram.

Far below come insects and spiders, which never weigh more than two or three ounces. Most of them are much smaller. Even ants half an inch long are well below a gram in weight. The biggest ant-colonies have about a million inhabitants; all this population together weighs no more than a large man. As for fleas, three average fleas go to a milligram. If you bought an ounce of fleas, you would have the pleasure of receiving over 80,000 of them. Even the solid queen hive-bee weighs much less than a gram, and the workers only about one-seventh of a gram—200 to the ounce. (An ounce is 31·1 grams.)

At the bottom are the rotifers, whose greatest giants fail to turn the scale at ten milligrams. The smallest many-celled animals are male rotifers, some of which weigh considerably less than one-millionth of a gram, so that it would take over a thousand to outweigh a single one of our muscle-fibres.

On the whole, the lower limit of size among the various groups is a good deal more constant than the upper. It is interesting to find that here again the limit for vertebrates is far above that for any other group. There is clearly a limit set to a many-celled animal in the number of cells out of which it is constructed; the smallest worm must have several thousand cells to build its organization. But it seems to be impossible, or unprofitable, to build a vertebrate out of less than several million cells (Figs. 15–20).

The small scale on which such a complicated beast as an

insect can be constructed is amazing. There are insects, complete with compound eyes, three pairs of jointed legs, wings, striated muscles, brain and nervous system and all the rest, which weigh less than the human ovum, and much less even than the nucleus of some large protozoa! A list of animals in order of weight would be full of surprises for most readers—a polyp as tall as a sheep, a frog as big as a terrier, a snail that lays eggs as big as a sparrow's. But we must leave mere curiosities on one side, and see whether we can find any thread of principle running through the tangled facts.

There exist definite biological reasons which limit the size of different groups. Insects are kept tiny by the fact that they breathe by branching air-tubes, not by lungs. Birds that fly cannot go above a certain moderate size for aerodynamic reasons; ostriches and moas show that birds can grow big if they sacrifice their wings. (Angels, by the way, are a biological impossibility. To obtain the motive force for flapping his wings, a normal-sized angel would have to have a breast-bone and breast-muscles projecting four feet from the front of his chest.) Land-vertebrates are limited by their leg-bones. The supporting power of a pillar of bone is proportional to its cross-section. A little thought will show that the weight of an animal's bones will have to go up faster than its total weight if its limbs are to continue to support it. The bones of Swift's Brobdingnagians would have snapped under their weight if they had been mere enlarged scale-models of normal men and women. And there is clearly a limit to the amount of mere supporting material which living muscle and blood can economically move and nourish. In water, however, almost all an animal's weight disappears; bones are needed as scaffolds and levers, no longer as supports. And so water-vertebrates can grow to a far greater size than can their terrestrial cousins; their size is limited only by the exigencies of food-supply and digestion.

Crustaceans, though aquatic, never grow really big, judged

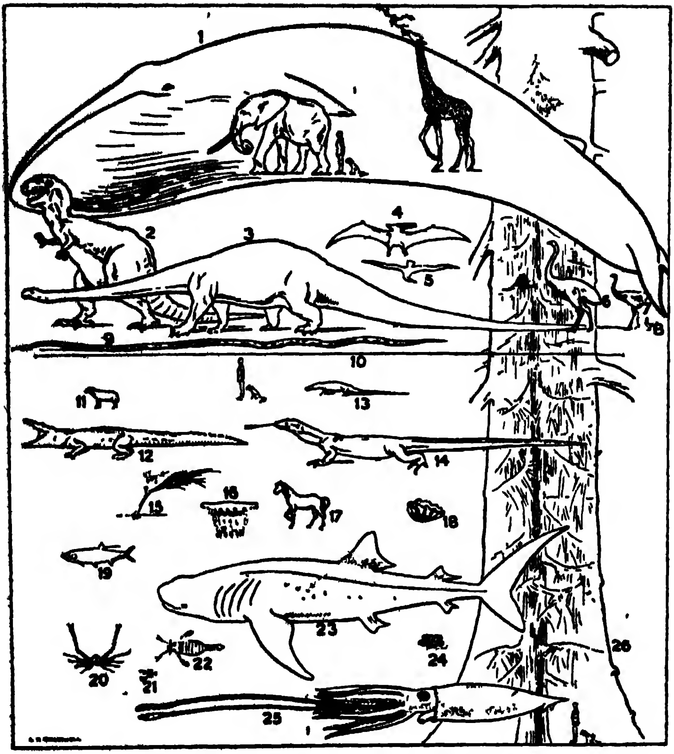

FIG. 15.—THE SIZES OF ORGANISMS. (A) The biggest living things.

All the organisms are drawn on a uniform scale. (1) Largest known animal (sulphur-bottom whale), with African elephant, man, dog and giraffe superposed; (2) Tyrannosaur; (3) Diplodocus; (4) Largest flying reptile (Pteranodon); (5) Largest flying bird (albatross); (6) Largest extinct bird (Aepyornis); (7) Ostrich; (8) Hen; (9) Largest extinct snake; (10) Length of largest tapeworm found in man; (11) Sheep; (12) Largest living reptile (West African crocodile); (13) Largest living lizard ("Komodo dragon"); (14) Largest extinct lizard; (15) Largest single polyp (Stomphiocerianthus); (16) Largest jelly-fish (Cyanea); (17) Horse; (18) Largest bivalve mollusc (Tridacna); (19) Large tarpon; (20) Largest crustacean (Japanese spider-crab); (21) Largest lobster; (22) Largest sea-scorpion (Eurypterid); (23) Largest fish (whale-shark); (24) Largest flower (Rafflesia); (25) Largest mollusc (deep-water squid, Architeuthis); (26) Bottom 105 feet of largest organism (California Big Tree), with 100-foot larch-tree superposed.

by vertebrate standards. In this case it is the habit of moulting which seems to be responsible. For, if you are a lobster or a crab, the bigger you grow, the longer it takes to produce an adequate new outfit of armour; a crab as big as a cow would have to spend most of its life in the retirement of the moult, hardening its hundredweight of shell before it could venture out and feed again.

Far down the scale, all creatures that move by cilia are kept extremely small. Not only can these hair-like rudiments of limbs never be more than microscopic themselves, but they are confined to the animal's surface, and cannot be massed in solid three-dimensional organs like muscles.

When ciliary-swimming marine larvæ seek to take advantage of the rich food at the sea's surface to grow to a larger bulk than usual before transforming into bottom-living creatures, they have to increase their cilia-carrying surface. In sea-urchin larvæ, this surface is a band of tissue bearing especially large cilia, which is braided, as it were, over the creature's protruding arms. In this case new surface is provided to cope with increasing size by growing new arms. In sea-cucumber larvæ there is a similar band of cilia, but they have no arms. And in these, increase of total bulk is accompanied by the throwing of the band into lappets and folds, often of extraordinary complexity.

The limit to the employment of cilia comes in creatures only a few millimetres long, like young tadpoles. When these are first hatched out they have not yet the use of their muscles, but are covered all over with cilia. By the aid of these they can glide very slowly over the bottom, but are completely incapable of swimming, or of any rapid movement. (The speed of ciliated animals under the microscope is apparent only; the instrument magnifies their speed as well as their dimensions.) So it comes about that no free-swimming ciliate can grow heavier than about a milligram. Sedentary creatures that use cilia for feeding can grow much larger. The limit comes with Tridacna, the giant clam; but very few reach a pound weight.

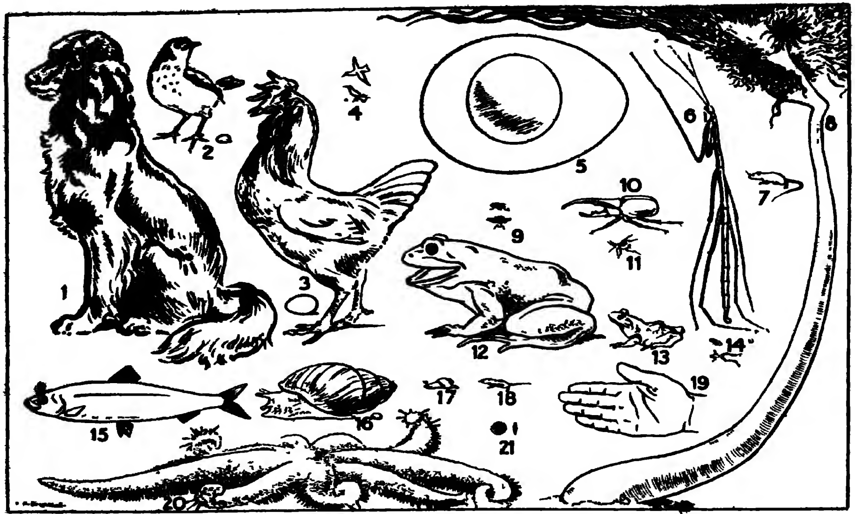

FIG. 16.—THE SIZES OF ORGANISMS. (B) Medium-sized creatures.

Nos. 3 and 8 are the same as those shown on Fig. 15,.Nos. 8 and 15. The dog can be seen at the bottom right-hand corner of Fig. 15. (1) Dog; (2) Song-thrush with egg; (3) Hen with egg; (4) Smallest bird (humming-bird) with egg; (5) Largest egg (Aepyornis); (6) Largest stick-insect; (7) House-mouse; (8) Largest polyp (Branchiocerianthus); (9) Queen-bee; (10) Largest beetle (Goliath beetle); (11) Common cockroach; (12) Largest frog (Goliath frog); (13) Common grass-frog; (14) Smallest vertebrate (a tropical frog); (15) Common herring; (16) Largest land-snail (Achatina) with egg; (17) Common snail; (18) Smallest mammal (flying shrew); (19) Human hand; (20) Largest starfish (Luidia); (21) Largest free-moving protozoan (Nummulite: extinct).

Efficiency of circulatory, supporting, digestive and excretory organs—all are needed for any great size to be attained. Flatworms, with their lack of blood, can only grow more than microscopic by spreading out flat like a leaf; and even then their size depends on the degree to which their type of gut can be made to branch.

Then we must remember some curious consequences of smallness and bigness. The very smallest living things are so tiny that they are not out of the range of influence of mere molecules. Even if you are down to a bare ten-thousandth of an inch across, so many molecules are hitting you that the bombardment is equal on all sides. But reduce your bulk a hundred times further and the rush of molecules may impinge with varying intensity, now on one side, now on the other, and what to all bigger creatures becomes mere uniform pressure keeps the tiny particle all its life long in the incessant jerky motion called Brownian movement. Filter-passers are so small that they no longer sink in water; the force of gravity has become negligible compared with the molecular bombardment.

Many units up the scale, we come on a very different consequence of relatively small size. Have you ever seen an insect drinking? Probably not. Insects do not drink, or at least they do not drink like larger creatures, by going down to a pool and lapping up the water. And yet they may be thirsty; butterflies may not infrequently be seen settled in crowds on damp ground, sucking moisture through their trunks. The reason for this in all probability lies in their small size. They cannot drink from open water surfaces; they seek a film on solid particles. They are most of them so small that the surface-tension inherent in the surface-film of water—that skin of molecules which is strong enough to support a water-skater and even a needle—is more powerful than they. Everyone has seen little moths and gnats struggling vainly against the grip of the surface-film; and one of the recognized ways of ensuring a peaceful night in flea-haunted corners of the world is to stand naked on

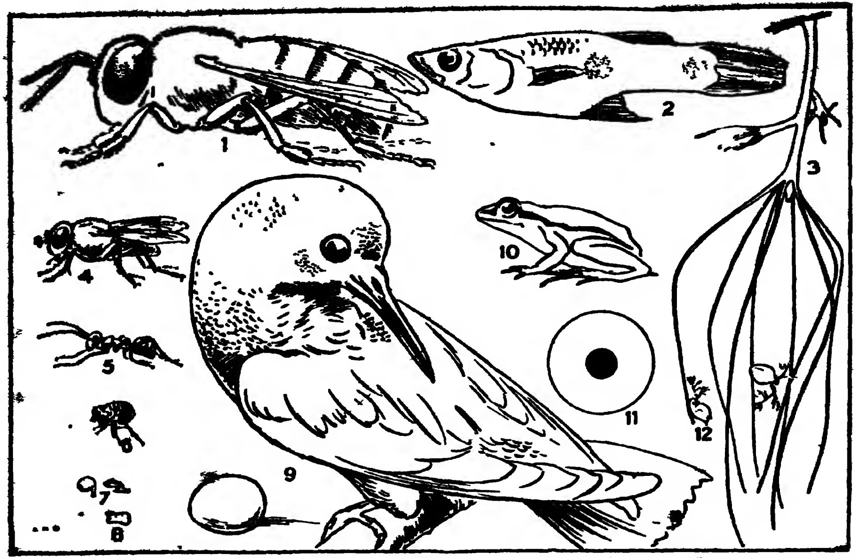

FIG. 17.—THE SIZES OF ORGANISMS. (C) Small naked-eye creatures.

Nos. 1 (queen-bee), 9 (smallest humming-bird and egg), and 10 (smallest vertebrate) are those shown in Fig. 15, Nos. 9, 4 and 14. (2) Smallest fish (Lebistes); (3) Common brown Hydra, expanded; (4) House-fly; (5) Medium-sized ant; (6) Common flea; (7) Smallest land-snail; (8) Largest ciliate protozoan (Bursaria); (11) Egg of common grass-frog in its jelly; (12) Common water-flea.

a tray in the centre of the room, let the fleas jump on to you, and then sluice them off with water. For all their jumping powers, the surface-tension holds them tight; and to get away once they are wetted, they have to lift many times their own weight of water. As J. B. S. Haldane puts it: "An insect going for a drink is in as great danger as a man leaning out over a precipice in search of food."

Thus to insects and spiders the dangers of drinking are very real; and most insects get their drink in their food, or sop it up from wet earth as we might suck moisture out of well-wetted blotting-paper, or at most suck at very small drops of it; and then generally through a long proboscis. It is possible, too, that a curious fact in insect anatomy is to be explained by their difficulty in getting drink. Their excretory organs are unlike those of all other animals in opening into their intestine instead of direct to the exterior. Our own large intestine absorbs water from the undigested food. If this is the case with insects, too, they waste no water in their urine.

But size, though it enables land-animals to laugh at surface-tension, makes them susceptible to the dangers of gravity. The smaller you are, the greater is the proportion of your surface to your weight, since surface goes up as the square of your length, weight as its cube. A big African elephant weighs about a million times as much as a mouse, its linear dimensions being about a hundred times greater. A little easy calculation will demonstrate that if an elephant could be re-cast, so to speak, into the form of a million mice, the same weight of material would now have a hundred times as much surface.

In a perfect vacuum, all objects, big or small, would fall at the same constantly accelerated speed. But in nature the resistance of the air comes in; and this depends on surface exposed. The huge proportion of surface to weight in the average bacterial spore means that it falls with incredible slowness; and even an average ant, though over a million times heavier, can hardly fall fast enough to achieve a real

bump. A mouse can be dropped down a mine-shaft, however deep, and arrive at the bottom dazed but unhurt. A cat or a dog will be killed, however. A man will be not only killed but smashed; and if a pit pony happens to fall over, the speed at the bottom is so terrific that nothing is left but a few of the hardest bits of its bones and a splash on the walls.

Size is also important in temperature-regulation, since the escape of heat is proportional to surface. For every gram of its weight, a mouse as big as an elephant would radiate away only one per cent. as much heat as a normal-sized mouse. Accordingly, the elephant has to have devices for increasing its surface so as to radiate away surplus heat: of these devices we shall shortly speak. In general, a small animal has to eat much more in proportion to its size to make up for this extra rate of heat-loss; and when the temperature gets very low it cannot manage to stoke up sufficiently. A big dog weighing forty-five pounds, for instance, for each pound of its weight needs only about half as much food to keep its temperature constant as does a small dog of seven pounds. A honey-bee would need 500 times as much; that is why bees cannot be warm-blooded. This explains also why small mammals and birds do not penetrate so far towards the poles as do larger ones. The smallest mammal in Spitsbergen is a fox; and there are scarcely any humming-birds that manage to exist outside the tropics or sub-tropics. For a similar reason, ears and other projections that increase surface are cut down to a minimum in cold climates; but in hot countries, where the need of the warm-blooded animal is not to conserve but to lose heat, they are often much enlarged, and provided with many blood-vessels. This is so, for instance, in the African elephant; when he holds his ears out from the side of his head, he is providing an extra fifteen per cent. of surface through which heat can be lost.

Still another bearing of size on structure is to be found in paddles and wings. As we have seen, with very small water-creatures, microscopic vibratile cilia will serve. In

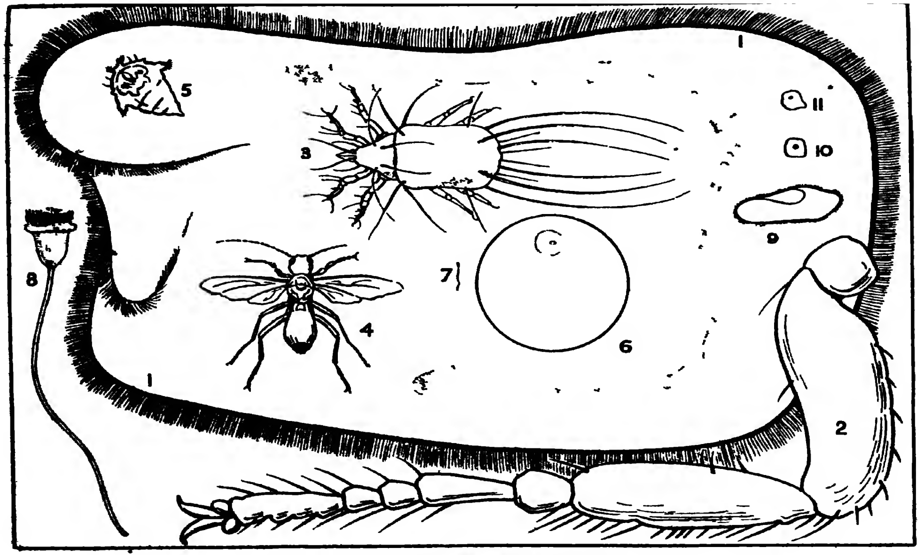

FIG. 18.—THE SIZES OF ORGANISMS.
(D) The smallest naked-eye creatures and some large microscopic animals and cells.

No. 1 (Bursaria) is the animal shown in Fig. 17, No. 8; No. 2 is the fore-leg of the flea shown in Fig. 17, No. 6. (3) Cheese-mite; (4) Smallest insect (Elaphis); (5) Smallest many-celled animal (male wheel-animalcule); (6) Human ovum; (7) Human sperm; (8) The bell-animalcule Vorticella, a ciliate; (9) Another ciliate (Paramecium); (10) Human liver-cell; (11) Dysentery amoeba. The dotted band in the body of Bursaria (No. 1) is its nucleus: it is much bigger than the smallest insect.

FIG. 19.—THE SIZES OF ORGANISMS. (E) Small microscopic cells and organisms

No. 1 (human sperm) and No 2 (human liver-cell) are the same as Fig 18, Nos 7 and 10. (3) Sleeping-sickness trypanosome; (4) Human red blood-corpuscle, with a malaria parasite inside it; (5) Red blood-corpuscle of frog, with nucleus; (6) Smallest free-living protozoan (Oikomonas); (7) A green flagellate (Euglena); (8) One of the largest bacteria (anthrax bacillus); (9) Typhoid bacillus, with flagella.

moderately tiny creatures that swim with limbs, the limb need only be a mere stump fringed with hairs or spines. As the animal grows, the main limb itself must be flattened and expanded, though a border of hairs may continue to be of service; and with further increase the limb grows more and more of a flat paddle, the hairs get relatively less and less important. The change is often made within the individual life-cycle of many crustacea. The same applies to flight. Many tiny insects fly by means of wings that are mere rods

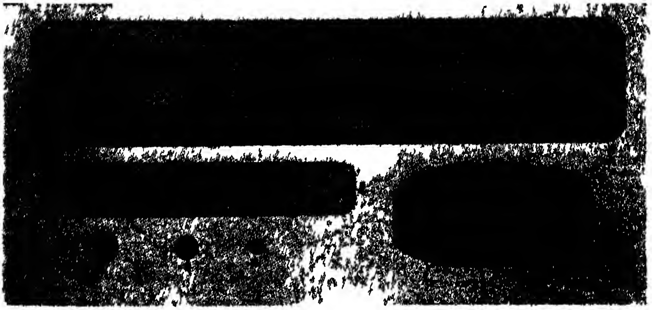

FIG. 20.—THE SIZES OF ORGANISMS. (F) The smallest organisms.

All are shown in outline. No. 1 (anthrax bacillus) is the same as Fig. 19, No. 8; (2) Tubercle bacillus; (3) Plague bacillus; (4) Bacterium of Malta fever (Micrococcus); (5) A particle at the limit of microscopic vision; (6) A filter-passing organism.

fringed with hairs. The lovely plume-moths are a little bigger; they work on the same principle, but multiply the hair-fringed rods. . And all flying creatures weighing more than a fraction of a gram must have a flat impervious expanse as their main or sole flying-organ.

There are some curious facts about the proportional size of parts in big and small animals. Eyes in particular always increase far more slowly than total bulk, because above a certain minimum size a small eye sees practically as well as a large one. The number of touch-organs in the skin also increases much more slowly than the bulk of the body. If

matters to a mouse to be able to deal with things the size of breadcrumbs, but such trifles do not concern an elephant; and the elephant accordingly has its touch-organs spread much more sparsely over its surface.

In animals of different size, but comparable intelligence, brains, for reasons we need not go into, increase roughly in proportion to surface and not to weight; so that mere percentage brain-weight is no criterion of intelligence.

§ 3

Colour and Pattern in Life

Hitherto in this volume we have been studying the adaptation of whole organisms to their habitats. It would be possible to embark upon an equally full and equally interesting study of the modification of single parts, isolated functions. Sight or digestion, the care of young or the capacity of producing sound, weapons of offence or organs of excretion—on any of such topics one could write an illuminating chapter of biological history. But space forbids us. We will here take the sole example of colour, that enrichment of the world, and deal with some of the biological uses to which colour and colour-pattern have been put. And we must leave it to our readers, with this sample to aid them, to use their imagination in reconstructing for themselves the richness and variety of life's functioning.

In this section then our topic is colour. We shall often use the word rather loosely to denote colour and pattern combined. We must also bear in mind that most animals are colour-blind, and that what to us is a pattern of colour, to them becomes degraded into mere black, white and grey; and also that most of the colours and patterns of organisms have been developed in relation to the eyes of other creatures, so that the colourings and patternings are not only not understood by their possessors, but may even be invisible and therefore non-existent to them.

A baby Ringed Plover fresh from the egg, which has never seen its mother, will, at the approach of danger, crouch and flatten with outstretched neck. In this position it becomes almost invisible in its native environment of parti-coloured shingle. But it cannot see itself or know what obliterative effect its actions have—as is indeed further demonstrated by the fact that it will crouch just as readily on grass or on a carpet, although there its behaviour merely makes it conspicuous. The egg out of which the baby plover hatched was equally protected by its coloration in the nest, although the hen-bird could neither know what colour her first egg would be, nor, even if she did, could she influence the way the glands of her oviduct would blotch on their pigments.

Some colours are, in their own right, useless. The most familiar case is that of our blood. Hæmoglobin happens to be so made that it looks red; but the redness has no value *qua* redness—it is a consequence of a particular chemical composition. Once there, the redness of blood may be used for the sake of its colour-effect, as in the comb and wattles of the barndoor fowl, or in our own cheeks and lips, or in the more lavish decorations of the baboon and the mandrill, who, as Mr. P. G. Wodehouse flippantly but expressively puts it, "wear their club colours in the wrong place." But in origin it is accidental. Other colours may have a physiological but not a biological meaning—the colour may help in achieving some function of the body. The most obvious example here is the green of plants. They are green because of their chlorophyll; and their chlorophyll is green because it absorbs the red and the violet parts of the spectrum to obtain energy for pulling the carbon out of carbon dioxide. There must be some reason why it does not absorb green light as well, but we do not yet understand it. If it did absorb all wave-lengths, the prevailing colour of our landscapes would be not green but black; and it is probable that we should have found in black the same qualities of freshness and restfulness that we now find in green. But the colour is

green, and it has meaning in relation to its own chemical functions, not in relation to other organisms.

The pigment of the skin in the tropical races of warm countries is equally physiological; it prevents the entrance of ultra-violet light in the excessive and harmful amounts poured down by the tropical sun.

Finally, we come to colour with biological function. The two prime functions here are either to reveal or to conceal. The former are usually called *sematic* colours, colours which point you out, the latter *cryptic*, colours which hide you. In the earlier chapters of this volume we have talked of many concealing colours, especially those which harmonize the general tint of the animal with the general tint of its background (white in the arctic, green in the forest, sandy in the desert, blue on the surface of the sea, dark red or black in the abyss). Besides such general resemblances, animals may show protective resemblance to particular objects. We have the stick-insect, drawn out in fantastic fashion; the stick-caterpillars of many geometrid moths, which hold themselves rigid all day in amazing likeness to a twig (complete with buds), only moving in search of food when the sun goes down; the leaf-insect, which not only has its body transformed into the likeness of a green leaf, but bears little green leafy frills on its legs; the famous Kallima butterfly, which at rest not only is coloured brown like a dead leaf, and shaped complete with stalk and pointed tip, but has mid-rib and veins drawn on it, and in some species blotches that simulate mould spots, and even transparent patches bare of scales to look like holes; the little moths that escape unwelcome attention by a resemblance to a small bird's white dropping; the sea-horse whose strange garb of rags and tatters makes it look like a piece of the Sargasso weed among which it lives.

One of the most remarkable cases is that of a South American species of nightjar. All nightjars and nighthawks are protectively coloured, they and their eggs and their young; the common European species has, in addition, the habit of roosting crouched down lengthways along a branch,

when its attitude and its mottled plumage make it seem one with the tree. But this South American nightjar goes one better. It nests in hollows on the top of tree-stumps or fence-posts. All day it broods in this exposed situation, but is very rarely discovered owing to its delicately pencilled grey coloration and its extraordinary habit of sitting bolt upright with head pointed up in air, seeming to be only a projecting bit of dead wood. If you approach, it shifts imperceptibly round, always facing you. When the young is hatched and grows too big to be brooded, it too adopts this same pose, and lives all day in this perpetual rigidity until it is able to fly. A combination almost as striking is seen in the bitterns, which, when alarmed, lift their beak and neck vertically in air, and by always fronting the intruder with their striped breast, manage to fade into invisibility in the reed-beds which are their home.

Sometimes concealment is achieved by colour-change. The chameleon is the most famous example, but his powers have been much exaggerated, and are surpassed by other animals. Many tree-frogs become green when on leaves, brownish-grey on a branch; and in some cases at least the change of colour is achieved successfully even by blind animals.

But the facts in lower vertebrates are rather complicated, because besides apparently protective colour-changing, there are changes in response to such purely physical factors as the warmth, humidity and darkness of the surroundings. Put one frog in a dark moist jar and another in a white dry jar, and examine them after a couple of hours; the first will be strikingly darker than the second. Professor Hogben has demonstrated very neatly that this is an internal secretion effect. The colour-change is due to the expansion or contraction of little black cells in the skin, and these movements are controlled by the amount of secretion which the pituitary gland at the base of the brain pours into the blood, in response to messages from eyes and skin.

But flat-fish take the prize for concealment by change, for

they can change pattern as well as colour. In the Plymouth Aquarium is a tank with two communicating compartments, one floored with fine sand, the other with boldly-variegated shingle; in the tank are flounders, and visitors are invited to drive the animals from one compartment to the other and watch the results. In the shingly half, the fish are coarsely blotched with dark brown, sandy yellow and pale cream; but if one of them be chased through on to the sand, in less than five minutes its blotched pattern will have given place to a fine-grained uniformity, and the fish presents as good an imitation of its new background as it did of its old.

We must now turn our attention to pattern. A vast number of animals are lighter below than above; this is the simplest case of a concealing pattern. Its use is illustrated by an admirable model in the Natural History Museum in London. In a box, against a light-brown background, is a rough model of a duck, strongly illuminated from above. Although the duck is dark-brown above, and nearly white below, it blends wonderfully with the background, because the shadowed white of the belly becomes of the same tint as the illuminated brown of the back. But the model has a handle attached to it. Turn it upside-down, and the duck stands out strikingly, the white made brilliant, the brown turned almost to black. Essentially the same thing is seen in nature, whenever a fish swirls over on to its back; all but invisible before, it gleams into brilliant conspicuousness.

When an animal habitually lives in an unusual position, its shading is often correspondingly adjusted. There is a Nile cat-fish, *Synodontis*, that normally swims upside-down. Though this habit had already attracted the attention of the ancient Egyptians, we do not yet understand why it has arisen; but whatever its meaning, the shading of the fish has changed with it, and its upper side, though the belly, is darker. Still more curious is the case of the crustacean Anilocra, an external parasite on the body of small fish. It always clings parallel with the fish's body, and one longitudinal half of it is dark, the other light, to match the shading of its host.

In animals living against an irregularly-patched background this irregularity is sometimes wonderfully simulated; one has only to think of the lizards, moths, beetles and other insects that imitate to perfection the rough and lichen-encrusted bark of the trees on which they crawl or sit; or the brooding woodcock whose brown plumage streaked freakishly with yellow makes her almost undiscoverable among the sun-flecked herbage and dead grass where she nests.

The woodcock introduces us to a new principle—the principle which underlies the art of camouflage. It is interesting that it was first fully stressed by a student of animals—Thayer, artist and naturalist, whose book, *Concealing Coloration in the Animal Kingdom*, if often over-enthusiastic (we cannot follow him, for instance, in believing that the scarlet of the flamingo is of use as a concealment when flying against a sunset sky!), is yet, in its way, a classic. He was the first to realize the value of what may be called *ruptive coloration*—bold pattern which breaks up the form and outline of an animal into irregular and meaningless pieces. Very conspicuous in a museum case, such animals in nature are among the best disguised. The same principle, in exaggerated degree, was adopted for concealing guns, ships, and so on in the War. As an anti-submarine measure, an interesting variation was adopted. Ships were painted in bold patterns, usually in black, white, and blue, so as to give, through false perspective effects, a wrong idea of their course; and this made it much harder for the submarine to take up the correct position for attack. For a crouching animal, falsification of outline is valuable; for a ship threatened by submarines, falsification of direction. The dappling of many deer, the spotting of the leopard and ocelot, the striping of the okapi, and the pattern of the great boas and pythons may help in this way as well as by simulating sunflecks in the forest. Even the Malayan tapir may benefit by his white hinder-half.

It is worth mentioning that, as one would expect, all

spotted forest-dwellers show light flecks on a darker ground (simulating sunflecks), while any spots in desert-animals are always dark on a lighter ground (simulating pebbles or local shadows against the glaring sand). But the most striking examples of ruptive coloration are afforded by bars and stripes, which cut across the animal's true form and take the eye from its outline. Many tree-frogs practise this. A more familiar example is the ringed plover, so common on the beaches of Europe. Its black colour and head-stripe disrupt its lines and make it blend with the background in a most unexpected way. Its American relative the killdeer is very similar; and in the turnstone the trick is played for all it is worth, the bird in the hand looking a regular harlequin, but achieving invisibility on a rocky shore.

Camouflage may be either protective or aggressive. Of aggressive disguises the most wonderful examples are the flower-spiders and flower-mantises, which frequent flowers in order to prey upon the insects which visit them, and escape notice by being dressed in the same brilliant colours as the flower.

It is but fair to say that many naturalists and sportsmen have severely criticized the whole theory of concealing coloration, and while some, like Thayer, would make all coloration concealing, others would go to the opposite extreme and deny that any colour or pattern ever concealed its possessor. The truth, as so often, is between the two extremes. Many colours do not have a concealing but a revealing function; many others seem to have no function at all. But one need only have been an amateur birdsnester or a collector of butterflies and moths to know what protection colour may afford, while such marvellous adaptations as those of leaf-insects or bark-beetles or weed-like sea-horses may be best left to speak for themselves.

We now pass to our second main type of coloration—the coloration which reveals instead of concealing. First, there are the colours which help in recognition. The most familiar is the tail of rabbits, useless for all ordinary caudal purposes,

but so white and conspicuous that in America it has earned for its possessor the name of cotton-tail. Its functions seem to be to act as a danger-signal and to guide others to safety. A band of rabbits is feeding as dusk begins to fall. One or two scent danger; out flashes the white signal and, as they run to their burrows, marks the path to home. At once the rest are on the alert; and the young and inexperienced run no risk of growing confused or forgetting which way to run. It is sometimes argued that the white tail is a handicap instead of an advantage, since it gives a nice mark to the sportsman. But this is unbiological. The white tail was evolved millennia before guns or even men were thought of. That it renders its possessors temporarily more visible to a pursuing fox is no matter, provided it helps them to disappear into burrows or brush before the enemy has caught them.

A case where colour links parent and young in a special relation is seen in the great majority of birds with helpless nest-fed young. The inside of the young bird's mouth is almost invariably of brilliant colour, often yellow, though some, such as ravens, show a rich crimson, and others reveal striking patterns. As soon as the parent returns with food, up go the skinny necks, and open fly the large and brilliant gapes, making the destination of the food very conspicuous. In hole-nesters, like tits or wrens, this may be of real service by preventing waste of food and time. But in most birds we may hazard the guess that the adaptation is one of those which are of no service to the species, though a *sine qua non* to the individuals of which the species is composed. Watch any small bird feeding its offspring; it does not waste any time seeing that all take their turn, but jams packets of food down the throats that most obviously present themselves. Imagine one baby blackbird or robin of a brood unprovided with a yellow maw; it would not be so conspicuous, and would not be fed so often. It would thus grow more slowly and (since the rule that "unto him that hath shall be given" holds for birds as well as men) would so become still more

handicapped in the struggle for prominence when food was brought; it would run the risk of being suffocated, of being the first to starve if there were not enough food to go round; it would get a poorer start in life than the rest. The bright mouths of nestlings have been developed through competition between brothers and sisters; they are the result of selection, not merely within the species but within the family circle.

Then, oddly enough, there are animals which are conspicuously coloured because they actually want to get eaten. A certain percentage of the black-caps, sparrows and other passerine birds that we see around us are infested in their bowels with the fluke known to biologists as *Distomum macrostomum*. It is not a violently harmful fluke. It uses some of the bird's food and slightly damages the lining of its intestine; it is a nuisance rather than a danger. The birds were infected with the parasites when they were still nestlings, and we propose to note the manner of their infection as an example of what we may call appetizing coloration, and an illustration of Nature's impartiality.

The flukes, when they are mature, lay copious eggs, after the manner of internal parasites. The eggs pass out of the host bird with its excrement, and thus they are scattered over the leaves of bushes and herbs. Most of the eggs are wasted and come to nothing; a few of them, however, have the good fortune to be swallowed, with part of the leaf on which they rest, by a snail. The snail, we may note, must belong to a particular species, *Succinea putris*; in any other kind the eggs are digested and killed. But in *Succinea putris* they hatch out into microscopic, active larvæ. The larva bores through the snail's stomach and makes its way into his body tissues. There it comes to rest and undergoes a curious development. It grows enormously and becomes a shapeless radiating web of living tissue without brain or eyes or any of the usual marks of living animals. It spreads through the snail, growing at his expense, and becomes so mixed up with his tissues that it is difficult or impossible for a dissector to

separate it completely away. But in the front, by his head, it sends out special shoots. It sprouts out into lobes which grow up into his horns and distend them, and are very conspicuous from outside—partly because they are gaily coloured, with green and white bands and vermilion tips, and partly because they wriggle and pulsate actively just under the skin of their host. They are designed, in short, for being eaten; conspicuous as they are, they catch the eye of insect-eating birds, and since they distend the horn they prevent its withdrawal into the shell. Wherefore, sooner or later, they are pecked off by the next host. Each of these gaily coloured, attractive morsels is really a hollow bag containing hundreds of fluke eggs.

Now comes a curious development. If the bird swallows his mouthful, the bag with its contained eggs is simply digested away; it comes to nothing. But if the mouthful is carried back to the nest and given to the young birds, the fluke eggs, which can resist the milder gastric juices of the nestlings, hatch and infect their new hosts. So back to the beginning of the cycle again. And meanwhile the snail grows a new horn, and the parasite within him grows a new protrusion into it to attract another bird.

The curiosity of animals is often played upon by man. When we bait for mackerel with a bit of red flannel we emulate the fishing-frog; and in past decades the hunters of the American "antelope" or prong-horn often lured it within gunshot by gesticulating and behaving in other odd ways. There are also well-authenticated stories of small carnivores such as stoats or weasels playing strange antics and so luring inquisitive rabbits and other small deer within reach.

But the majority of revealing colours have the opposite intent; they advertise distasteful qualities and fall under the head of *warning coloration*. An everyday example is afforded by the wasps and hornets, with their conspicuous banding of black and yellow; black-and-yellow, too, are the caterpillars of the cinnabar moth, which are rejected incontinently by

almost all birds. The black-and-yellow fire-salamander is equally conspicuous; and he is equally nauseous, owing to the milky secretion of special glands in his skin, which is actually fatal to small animals. The poisonous coral snakes are ringed with brilliant black, white and red; a number of butterflies, which experiment has shown to be rejected on account of their acrid taste or their tough consistency, are large, slow-flying, with showy and definite patterns.

The meaning of these devices is clear enough. Lloyd Morgan made experiments with cinnabar caterpillars and chicks fresh from the incubator-drawer, which showed that the chicks have to *learn* that the caterpillars are nasty. A single lesson is often enough. The burnt child dreads the fire: ever afterwards the sight of the beast is sufficient reminder to prevent the chick from trying it again. All enemies who can learn must be taught by experience; and a certain number of the nauseous or noxious creatures are sacrificed for the good of their brothers and cousins in order to educate their enemies. The individual dies for his cognates. The advantage is to the group.

Warning coloration cannot afford to be subtle or refined. The conspicuous colours serve to make the process of education as easy and rapid as possible, and, by sharply distinguishing the inedible from the edible, make subsequent mistakes less likely. In the domain of sound, the rattle of the rattlesnake and the hiss of other serpents serve the same warning function.

The skunk is the typical instance of warning coloration, as it is certainly the closest relative of man to practise the device. Everyone knows the power of the skunk's weapon; how dogs bedewed with the vile liquid run off in howling despair; and how no wild creature, however large, ferocious or hungry, will touch a skunk. Skunks most effectively combine appearance and behaviour for warning purposes. They have not adopted the ordinary principle of shading; white above and dark below: their form stands out sharply against the background. The animal knows no fear, but

walks slowly, refusing to give ground or to run from man or beast. The white and bushy tail is held aloft as a warning banner. This fearlessness, justified by past conditions, leads at times to grave inconveniences in the face of modern inventions. A skunk will not make way even for a train, and a train is unable to step aside for a skunk; the resultant casualty may cause serious distress to the passengers for many hours.

But if enemies can learn the association of certain patterns with danger or distastefulness, and let their owners alone for the future, what is to prevent other animals from practising a simple bluff, and achieve immunity from attack by imitating the warning colours, without the trouble of developing the weapon or the offensive taste? The answer is that there is nothing to prevent it; natural selection can achieve any device, provided it is within the resources of life and of service. The only special condition is that the species which bluffs shall be much less common than the species with true warning coloration; if their proportions were the other way round, the lesson of the warning colour would never be properly learned. Such imitation of the outward appearance of a protected by an unprotected animal is called mimicry, and the species mimicked is styled the model.

Some of the best-known examples are the clear-wing moths, which closely resemble bees and hornets. Another is afforded by the two well-known American butterflies, *Danais plexippus*, the Monarch, and *Basilarchia archippus*, the Viceroy. The nauseous, flaunting Monarch is the model. It is geographically an invader, and geologically a recent invader, of America. The Viceroy mimic is a member of a quite different family, the Nymphalines, which are strongly represented in Europe and North America; it is so closely related to an American species of White Admiral that the two, in spite of their entirely different pattern, will interbreed and produce hybrids. The likeness to the model only holds for the adult stage; egg, caterpillar and chrysalis are all of regular White Admiral type. If mimetic likeness were

the result of local conditions of life, we should have expected the invading Monarch to have become modified in the direction of the native forms rather than vice versa; but if it is an adaptation on the part of the model, the facts are at once intelligible.

It is worth while studying the methods by which the mimic's likeness to its model is achieved; for they throw light on the processes of Evolution. The salient facts are, first that the resemblance may be produced in all sorts of ways; and that so long as the enemy's sense of sight is deceived, it does not matter what tricks are employed. In Brazil, for instance, there is found a sand-wasp, *Pepsis*, together with two mimics, a plant-bug and a long-horned grasshopper. The wasp's antennæ are short and thick; the mimics have the base of their antennæ thickened to look like the whole of the wasp's antennæ, while the rest is reduced to a filament so thin as to be invisible at any distance. Again, there is a distasteful group of South American butterflies which have prominent transparent areas on their wings; they are mimicked by a number of other butterflies and day-flying moths. In the models, the transparency is produced by the scales being reduced to minute vestiges. In some of the mimics, the same device is adopted, in others the scales are of full size, but enormously reduced in number; in others they are of full size and full number, but are themselves transparent; while in still others, they stand up on edge and so let the light pass through. In some clear-wing moths, on the other hand, the scales are loosely attached, so that they come off during the animal's first flight.

Examples such as these show how impossible it is to suppose that the conditions of life directly bring about the mimetic resemblance; any kind of Lamarckian explanation is ruled out of court, and as the only possible agency for the origin of mimetic adaptations, we are left with natural selection guiding random variation. The same reasoning holds good for the highly original method by which the plant-bug *Heteronotus* achieves its mimicry of ants. The roof of

the front segment of its thorax is prodigiously expanded so as to cover all the rest of the animal, and modelled into the colour and shape of the top half of an ant !

The Membracidæ, the family of bugs to which Heteronotus belongs, provides in itself a remarkable object-lesson in deceitful adaptations and their origin. All of them have their first thorax-segment expanded into some sort of shield, often with no obvious adaptive significance. But this convenient expansion, once it is present, has been used as the raw material out of which all sorts of resemblances, both for concealment and for mimicry, have arisen. In one species, it is prolonged fore-and-aft to look like a grass-seed ; in another, it is converted into a hollow semblance of a thorn, below which the little bug crouches against a stem ; in another, it looks like a hook burr ; in Heteronotus, as we have seen, it takes the likeness of an ant ; in Oeda it is much swollen and coloured bright orange, to mimic very exactly the cocoon of a distasteful moth. The whole group is defenceless and palatable ; they all possess the thoracic shield which can be moulded into the most fantastic shapes without change in any of the vital organs ; and so resemblance of one sort or another has become their main method of defence. In every case the resemblance is a hollow sham, and the general structure and habits of life are left unaltered.

In some cases, a single individual may pass from one sort of mimicry to another during its growth. The grasshopper *Eurycorpha* when young mimics ants, thinning its antennæ to invisibility, painting-in a waist, and having the instinct to run about restlessly, ant-like, among its models. But as it grows up, it becomes too big to look ant-like : and finally moults into a green creature with expanded wings, which escapes detection by its leaf-likeness and its immobility. To pass from the likeness of an ant to that of a leaf, however, it must go through an awkward intermediate stage when it resembles neither the one nor the other. At this age it is provided with yet a third set of instincts, and tries to escape from its enemies either by hiding or by " shamming dead."

The cuckoos provide us with one of the few examples of aggressive mimicry, in which a resemblance serves for the direct exploitation of the model. The common European cuckoo exists in a large number of strains or races, each of which lays its eggs almost wholly in the nests of one kind of dupe; the meadow-pipit cuckoos and hedgesparrow cuckoos are the commonest strains in Britain, while in some parts of Europe there are redstart cuckoos, and in Japan, bunting cuckoos. In some cases the cuckoo's eggs are not particularly like the dupe's eggs; but usually the resemblance is striking. Recent investigation makes it almost certain that the differences are due to differences in the severity of selection. Sometimes the dupe is easy-going and stupid, like the hedgesparrow, and will brood almost anything; then there is no need for the cuckoo's eggs to resemble their hosts, and no resemblance is achieved. This is not because of any difficulty in the cuckoo's producing a blue egg like that of the hedgesparrow. Redstarts also lay blue eggs. But they are stricter and will turn suspicious-looking objects out of the nest; and the cuckoo-strains that parasitize them, having been rigidly selected for egg-mimicry, lay blue eggs. The same is true for buntings, even the strange and unusual scribble-patterns of their eggs are copied by their cuckoo-parasites. The resemblance is protective so far as it concerns the eggs themselves. But it is aggressive from the point of view of the race; the egg, once preserved from expulsion, produces the ugly little nestling which in the common cuckoo destroys all its foster-brothers, in other species appropriates a share of their food.

Finally, we cannot pass over two extraordinary cases which show into what strange paths variation and selection may lead an animal. The palatable West African moth *Deilemera* spins a cocoon covered over with little white ovals. Any entomologist seeing this would say at once that these were the cocoons of Hymenopteran parasites, which, after devouring the interior of the just-transformed caterpillar, emerge to pupate on its exterior. These parasites' cocoons are very

tough and resistant, and are despised by most insectivorous animals. The average bird appears to be as readily deceived as the average entomologist, and so the Deilemera profits by its likeness to its deadliest enemy.

Then there is the case of the alligator-bug, *Laternaria lucifera*, one of the large insects of tropical America which are known as lantern-flies (Fulgoridæ). From the front of its head there projects forward a huge hollow structure, which has been turned into a mask admirably representing a miniature alligator. The "eye" and "nostril" are raised on knobs, as in a real alligator's head; they are painted on in black, and the eye has even a white patch simulating the reflection of light. Along the side is a dark line representing slightly opened jaws, and from this there stand out in relief the most convincingly white and flashing teeth. At first blush the difficulties in the way of accounting for such a resemblance in terms of natural selection, or indeed on any rational basis at all, seem insuperable. The resemblance is not to a whole alligator, but only to its head, and to the head of an unnaturally diminutive alligator; and even if the resemblance be useful now, what advantage could have been secured by the early and incomplete stages in its evolution?

This last question is not nearly such a hard nut to crack as it seems, for all lantern-flies have an enormous hollow expansion in front of their head. We do not know in the least what function the expansion may have, but there it is; and in some forms it has roughly the general shape of the imitation alligator-head in Laternaria. It needs little change to convert this projection into a rough animal mask, and if that be of advantage, then the final touches can be easily added later. As to advantage, that too is not so difficult. A bird or a little monkey picking over the foliage suddenly comes on an object which looks like a grinning reptilian head. Is it likely to go on with its exploration and taste and try?

There are, as a matter of fact, other lantern-flies with

less perfect animal masks, and masks which resemble not a particular creature, but serve their purpose by appearing simply vertebrate and ferocious. The effect here is based not on specific resemblance, but on general association. This particular form of bluff we may call associative mimicry or terrifying coloration. It is found in many insects, notably in their larval stages. A number of large caterpillars have prominent eye-like markings on either side of their body; when frightened, they draw in their head, puff out the eyed segments, and so provide themselves with a sufficiently vertebrate and alarming appearance to scare off some at least of their enemies. The caterpillar of the common puss-moth adopts a more curious method. It, too, puffs out its fore region, showing a prominent pattern; at the same time it erects its forked "tail" and from each fork protrudes a red and wriggling filament. In this guise it has startled many a juvenile collector, and doubtless many a bird. This particular appearance is not wholly bluff, for the puss-moth larva secretes formic acid, which it ejects as a last resort. The lobster-moth caterpillar assumes an even more grotesque appearance when alarmed.

There still remains, however, another type of mimicry to discuss. There are seven British species of wasp of the genus Vespa, and every one of them is banded with black and either yellow or orange-yellow. Black and yellow recurs as a warning colour in many other wasps, in several bumble-bees, in cinnabar caterpillars, in the fire-salamander. What is the reason for this recurrence of one coloration? Partly no doubt that it is a conspicuous one; it is not for nothing that the Automobile Association have chosen yellow for their motoring signs, and that yellow signals are beginning to oust the old red and green on some railways. But might there not be advantages also for a species to be hall-marked dangerous with a widespread and therefore already widely known pattern? The possibility is converted into a certainty by what we find among butterflies. Here warning patterns of a complexity which rules out the

FIG. 21.—THE FITTING OF MIMIC TO MODEL.

Left, the model, a distasteful African butterfly, *Amauris niavius*. Above is the sub-species found on the West Coast and across to Uganda. Below, that on the East Coast, which has much more white on its wings. The two in the middle are intermediate forms from the transition zone in eastern Uganda and western Kenya. Right, the mimic, a Swallowtail butterfly, *Papilio dardanus* from above down, female and male of West Coast sub-species; male and female of East Coast sub-species. The males are not mimics, and, although they become blacker on the East, the females become whiter, like their models.
(*Courtesy of Prof. Poulton and the Hope Department of Zoology, Oxford.*)

FIG. 22.—ADAPTATION IN MIMICRY AMONG AFRICAN BUTTERFLIES.

Left, models. The top four are Planema epæa; first a male and female of the West Coast sub-species, then a female of the Uganda sub-species, then a female of the Abyssinian sub-species. Below, the Abyssinian sub-species of *Amauris niavius* (cf. Fig. 21), a model belonging to another family. Right, mimics, all Swallowtails of the species *Papilio cynorta*. Above, male (not mimetic); next, West Coast female (mimics the West Coast Planema); third, female of Uganda sub-species (mimics Uganda Planema). As the female's normal pattern is nearer to the Amauris than the Planema model, in Abyssinia selection has moulded the mimic to resemble Amauris (below).

possibility of chance coincidence are often shared by a number of distasteful species. The species may belong to different genera or to different families, whose patterns are characteristically quite unlike, so that their ancestry would be expected to make them differ, not to resemble each other.

Bates had been the first to put forward a reasoned theory of our first type of mimicry—mimicry by bluff; but he was puzzled by this likeness, often very close, between

FIG. 23.—PROTECTION BY BLUFF.

Left, the Puss-moth caterpillar in normal attitude (above) and in the terrifying pose it adopts when alarmed. Its front view simulates a face and from its tail protrude red, waving filaments. Right, the Lobster-moth caterpillar in normal attitude (above) and terrifying attitude (below).

many distasteful species. It was reserved for Fritz Müller, following in Bates' footsteps in South America, to point out its meaning. The efficacy of warning colour in an insect depends upon the education of insectivorous animals; and to accomplish this education a certain number of individuals must be sacrificed each year for the good of the rest. If a number of species adopt a single hall-mark, the prescribed number of victims will be no greater, but the sacrifice will be spread over all the species instead of falling entirely on the shoulders of one.

The two types of mimicry are distinguished by the names of their discoverers. Mimicry by bluff is called Batesian, mimicry by pooling of warning colours is styled Müllerian. As Poulton writes: "A Batesian mimic may be compared to an unscrupulous tradesman who copies the advertisement of a successful firm; Müllerian mimicry to a combination between firms to adopt a common advertisement and save expense."

CHAPTER V

THE SCIENCE OF ECOLOGY

§ 1

Ecology is Biological Economics

WE come now to a fresh way of regarding life, by considering the balances and mutual pressures of species living in the same habitat. We have studied the forms of life, we have traced what we have called, perhaps rather clumsily, "biological invention," and the evolution of existing forms, and we have considered the adaptation of these forms to the exigencies of this or that habitat. In every habitat we find that there is a sort of community or society of organisms not only preying upon but depending upon each other, and that a certain balance, though often a violently swaying balance, is maintained between the various species so that the community *keeps on*. In this new chapter we are going to study this swaying balance.

The particular name given to this subject of vital balances and interchanges is called Ecology. Ecology is a term coined by Haeckel, the celebrated German biologist, in

1878; its root is the Greek οἶκος, a house, which is also the root of the kindred older word economics. Economics is used only for human affairs; ecology is really an extension of economics to the whole world of life. Man is always beginning his investigations too close to himself and finding later that he must extend his basis of inquiry. The science of economics—at first it was called Political Economy—is a whole century older than ecology. It was and is the science of social subsistence, of needs and their satisfactions, of work and wealth. It tries to elucidate the relations of producer, dealer and consumer in the human community, and show how the whole system carries on. Ecology broadens out this inquiry into a general study of the give and take, the effort, accumulation and consumption in every province of life. Economics, therefore, is merely Human Ecology, it is the narrow and special study of one aspect of the ecology of the very extraordinary community in which we live. It might have been a better and brighter science if it had begun biologically. Here, we hope to show that ecology lays the foundations for a modern, a biological and an entertaining treatment of what was once very properly known as the "dismal science" of economics.

§ 2

The Chemical Wheel of Life

Everywhere, except in phases of extreme geographical and meteorological change, the world presents in every habitat this swaying balance of diverse species, and everywhere we find that these communities which prey and depend upon one another present many resemblances in pattern. It is not altogether fanciful to compare all these various communities, each one to a sort of super-organism, and in practice much of the thought and work of the ecologist involves that idea.

We have already made it manifest that except for the

green plants (and possibly certain bacteria) no living thing can live upon any food except the substance of other once living things. The leafy green plant on the earth, the smaller green plants in the plankton of salt- and fresh-water, are the primary sources of all living substance. Every biological community exists on that as its basis. And as we have explained, the chlorophyll does its work by utilizing the energy of the sun. If animals and fungi are food-parasites upon green plants, green plants are energy-parasites upon the sun. The whole of life upon earth depends entirely upon solar energy. The sun's energy is the physical source of all life.

The great bulk of living substance is composed of carbon, hydrogen, oxygen and nitrogen. But a number of other elements, though present only in traces, are equally essential. There must be sodium, potassium, calcium, magnesium, iron, phosphorus, sulphur, chlorine, iodine, and perhaps silicon, copper and zinc.

Life's carbon is derived almost exclusively from carbon dioxide, which is present in the air to the average amount of 0·03 per cent. and is held in solution in all waters, but in very varying proportions.

Nitrogen enters green plants in the form of nitrates dissolved in the soil water or in the water in which they float. All the other substances which plants need for construction—phosphorus, sulphur, calcium, magnesium and the rest—are brought to them dissolved in water in the shape of inorganic salts.

Hydrogen enters the green plant in the form of water which is utilized with carbon dioxide in the manufacture of sugar. As we have described earlier, the oxygen of the carbon dioxide is split off and returned in elemental form to the air or water round the green parts of the plant.

So that, so far as the building up of carbon into organic substance goes, oxygen is a waste-product, there being sufficient in the water absorbed by the plant to cover all that is needed for the construction of sugars and other

carbohydrates and of proteins. But, of course, it is necessary to take in oxygen at another part of the cycle to sustain the slow fire of living oxidations that generates the energy required for the business of living. The oxygen to feed this slow flame is obtained by green plants in elemental form, either direct from the air or dissolved in water. The atmosphere serves the oxygen needs of the great bulk of animals and of non-green plants; there are, however, a few parasitic animals and a fair number of bacteria and fungi which manage to extract the oxygen needed for their energy-production from the organic substances on which they feed.

The green plant having effected this synthesis of organic carbon and nitrogen compounds, of which it alone is capable, the rest of life steps in to seize its share of the spoils.

Plant-carbohydrates and plant-proteins are the only vehicles by which carbon and nitrogen can enter the animal kingdom. They must be taken to pieces by the enzymes of the herbivore's gut before they can pass through into the real interior of its body, but the pieces must not (save in some protozoa) be of simpler chemical nature than sugars and amino-acids. Carbon or nitrogen presented to an animal in any simpler form is as useless as a pile of bank-notes to a man on a desert island.

Once the carbon and nitrogen have entered upon their animal career, they can continue to circulate in the animal kingdom as carnivore preys on herbivore and one carnivore on another. In the process, however, the complexity of the carbon and nitrogen-carrying compounds never falls below the level of simple sugars and amino-acids.

The handing on of these organic substances does not go on indefinitely. Some animals have no natural devourers; others escape devouring or die from disease or old age. Not all plants are devoured. The dead substance which would otherwise remain a locked-up accumulation of complex compounds, of no further use to life, undergoes dissolution. Some part of it undergoes purely chemical degeneration, some part of it is simply oxidized; but the

greater portion is broken up by *decay*—that is to say, by the action of special bacteria. Decay is a living process; it is part of the cycle of life; it is not a mere inorganic dismantling. A great variety of bacteria are concerned in it, each species playing its own part in the decomposition.

If decay, helped by the natural oxidations due to the oxygen in the air, proceeds to its limit, the carbon that once was life's reappears in the form of carbon dioxide, its nitrogen enters air or water as ammonia, and the other elements for the most part become converted into water and salts. In poorly aerated situations, however, the carbon may be given off as the marsh gas or methane (CH_4) that we see bubbling up from the bottom of stagnant waters, and the sulphur as hydrogen sulphide (H_2S) with its familiar stench of rotten eggs.

The materials in this course of decay may be utilized by still other organisms before reaching the final stage, and they may be once more directed upwards to greater complexity. Most moulds and fungi do this; they are in effect parasitic upon decay. Though they vary considerably among themselves as to the details of their nutrition, certain general features are always present. They cannot tap light-energy to win the carbon from carbon dioxide; and they find it inconvenient or unnecessary to utilize simple inorganic salts as source of nitrogen. But though food on the low chemical levels from which it can be hauled up into life by green plants is unavailable for them, they do not require it in such a complex form as is necessary for animal assimilation. They do not insist on sugars and amino-acids; they can utilize lower grades of chemical complexity.

Some fungi may fall a prey to animals and so lift the disintegrating compounds back to the full animal level, but in spite of this occasional upward return which fungi render possible, the vast bulk of living materials do at last deteriorate back to the extremity of decay. The carbon makes full circle and is once more available in carbon dioxide for the synthetic activities of green plants. The

ammonia or ammonium compounds, in which form the nitrogen mostly returns to the air (and also the far less abundantly generated sulphur compound hydrogen sulphide), form the basis for new activities on the part of bacteria. A series of bacterial species attack this ammonia, and through their vital processes convert its nitrogen into the form of nitrates, which again are available for the nutrition of green plants. Once more these elements enter upon an upward phase in the wheel of life.

The rôle of the bacteria is absolutely essential in this cycle. Without the agency of a horde of microbes belonging to a great number of kinds, and each restricted to one chemical job, to one step only of the whole transformation, there would be an unbridged gap in the vital circulation. Doubtless, given time enough, inorganic oxidation would decompose proteins and carbohydrates, just as it succeeds in rusting iron; but the turnover would be so slowed down that only a negligible fraction of existing life would be able to carry on, and there would be a much greater leakage of nutrient elements into wholly unavailable forms.

Thus life depends for its primal supply upon green plants, and for its sustained supply upon bacteria. The whole of life considered chemically is one cyclic process from green plant to bacteria and so again to green plant.

The cycle does not run smoothly. It runs with various leakages and blocks, whereby some of the food elements are changed into forms useless to the great majority of living things, or deposited in the solid state and so taken out of the reach of all life until inorganic solution or oxidation has made them again available.

Shortage of available nitrogen is a chronic state in life's affairs, and the formation from organic compounds of elemental nitrogen gas, chemically inert and so unavailable to almost all organisms, constitutes a serious leakage. Such a leakage is occurring all the time. Wherever insufficient oxygen is present, certain of the bacteria which normally convert ammonia into nitrates, can reverse their activities

and use nitrates as a source of oxygen, restoring the nitrogen into the air as a useless by-product. If this leak were to continue indefinitely, the wastage of available nitrogen could not be made good, and life would gradually perish of nitrogen want, though in the midst of an unavailable plenty of nitrogen.

However, the wastage due to such denitrifying bacteria is made good by means of yet another class of bacteria, the nitrogen-fixers, who are aided by the mycorrhiza fungi which we have already discussed in Chapter IV, § 1. By chemical means at present unknown, these plants can seize hold of the nitrogen of the air and transform it into vitally-available compounds—a feat imitated by man in recent years, but only with the expenditure of great quantities of energy, derived from water-power or other energy-sources. The nitrogen-fixing bacteria live for the most part in an association of mutual benefit with the members of the leguminous order of plants, the pea tribe. It is a symbiosis of great practical significance. The more leguminous plants, like beans, peas, lupins, clover and alfalfa, that man cultivates, the more nitrogen will he divert from the air back into vital circulation.

There are other types of leakage or block in the rotating wheel of life. Through a lack of sufficient oxygen during decay, carbon may be locked up in its elemental form, unavailable to green plants. Many cubic miles of carbon have been thus solidified in the form of peat, lignite and coal, and much of this food-capital has been idle, locked out of circulation, for hundreds of millions of years. It is not yet certain how the mineral oils which give man petrol and paraffin oil arose; but whether their origin is from plants, or, as is possible, from marine life, they again constitute a locked-up store of carbon that was once in circulation. The fire-place, the factory, and the motor-car are doing all they can to restore this deposited carbon to a state of gaseous accessibility.

Carbon may also be deposited uselessly in combination

with the important metal calcium. Considering that all chalk or limestone is entirely or almost entirely derived from the skeletons of living things; that an unknown depth of calcareous deposits, in the shape of Globigerina ooze, covers nearly thirty per cent. of the whole sea bottom, and that corals are steadily imprisoning tons of calcium in coral reefs every day, we might anticipate a general calcium shortage. The element is, however, so abundant that only in certain restricted areas of the land is calcium-shortage of serious import to life.

Guano, a deposit consisting of the excrement of bats and birds, is another example of locked-up material. Most excrement serves to enrich the soil on which it falls, but in the caves and rainless islands where guano is found the manure has been unused and has merely accumulated. Here again man comes to the rescue, and, by using guano as a fertilizer, restores its nitrogen and phosphates to the soil.

All these diversions of material into idleness are directly effected by or through life. In addition, purely inorganic processes may abstract quantities of this or that element from the rotation. Evaporation is the most potent of these agencies; evaporation has imprisoned many million tons of salts in the sterility of salt deserts and rock salt. The high prices given for fertilizers containing magnesium and potassium, sulphates and phosphates, indicate how serious to men such diversions of vital material from the wheel of life may be.

With such digressions and losses, with fluctuations and uncertainties, the wheel of life turns on. The driving force of the wheel is solar energy. By virtue of that energy, and of that energy alone, the elements are drawn into the wheel, pass from lower to higher complexities of combination, pass from green plant to animal, from one animal to another, live, die, live and die again and again; some fall by the wayside as waste masses of substance, some stay unutilized for millions of years, others are caught by a fungus or a bacterium and turned back to the higher levels

again; so sooner or later they return to the state of simple and stable combination at which they began, to be caught up once more by the sunshine and the chlorophyll and once more sent round the cycle.

§ 3

The Parallelism and Variety of Life-communities

This fundamental Wheel of Life turns in a multitude of places and under a vast variety of conditions, and each one gives us a different sort of life-community. The Wheel of Life is indeed rather like the work of some extremely popular playwright who has only one leading idea in his head, which he repeats again and again with no great originality or invention. The scenery varies—it is not his work—the costumes and the names change, new fashions soak into him, the cast of the actors is different and now one personality dominates and now another, there is a lack or a superfluity of supers for the minor parts, or some performing animal or other novelty has to be worked in, but beneath these changes we detect the same old plot and very much the same rôles.

We will consider now something of the variety and of the fundamental similarity of the life-communities thus evoked. They are, so to speak, organizations of species of organism. Life-communities develop and evolve as wholes. They might be called super-units of life. Always in a life-community there will be green plants as producers, herbivore animals (and parasitic plants) as exploiters of green plants, and decay-bacteria exploiting both and breaking down the substance of their dead bodies. Without the greenery, production would cease and the whole community come to an end. Without the decay-producing bacteria the return of plant-food substances would be so much slowed down that the whole drama would stagnate through the arrest of material in corpses.

Animals as well as bacteria speed up the circulation, for the urea and carbon dioxide into which they eventually turn the plant-food they eat are much more readily and quickly available for plants than the mere dead leaves and stems, full of wood and cellulose, that would be the main end of green plant substance if there were no animals to eat it. And even as corpses, animals are more speedily brought back into availability by decay than are the remains of dead plants. So, while green plants could exist by themselves as an independent life-community, carrying out a quite independent drama of transformations, yet animals are of the greatest importance as accelerators to such a cycle. They actually benefit the species of green plants whose individual bodies they devour alive or break down when dead, for without them the rate of growth of green plants would be enormously slowed down, and both their abundance and their variety would be infinitely less.

The life-community on land differs widely and necessarily from the more primitive life-communities of the sea. It has been said that "all flesh is grass and all fish is diatom," and while the life-community of the waters has its microscopic food-basis nearer the sunlight and carries out its interchanges in three dimensions, the life-communities of the land arise upon the soil and vary much more widely because of the diversity of rock and exposure upon which they live and have their being.

Among the green plants of every land-community there are usually one or a few dominant species much more abundant or conspicuous than all the rest—the oaks in an oak-wood, the grass in a field, the heather on a moor, the great trees in a tropical forest, the bulrushes in a swamp. But besides these, there are always plenty of other less abundant kinds which find rôles for themselves among the margin of opportunity which the dominant form leaves over. Each life-community thus comprises a vegetable hierarchy.

This fact that there must always be a dominant vegetable

type or types in any life-community comes about through the dependence of plants upon light and moisture. The kind of plant which, in the local conditions of moisture, can win in the struggle for light will in the long run kill out its main rivals or prevent them from reproducing and so rule the community. The climate may permit of forests; then the dominants will be trees. Or a dry soil may support nothing more than a steppe or a prairie; then the dominants will be grasses. In all cases the dominant is the kind of plant which can succeed in getting the biggest share of the light-energy streaming down upon the area.

Light being the main necessity of plants, the dominant plant of a community is the tallest member, which can spread its green energy-trap above the heads of the others. What marginal exploitation there is to be done is an exploitation of the dimmer light below this canopy. So it comes about in every life-community on land, in the cornfield just as in the forest, that there are layers of vegetation, each adapted to exist in a lesser intensity of light than the one above. Usually there are but two or three such layers; in an oak-wood for example there will be a layer of moss, above this herbs or low bushes, and then nothing more to the leafy roof; in the wheat-field the dominating form is the wheat, with lower weeds among its stalks. But in tropical forests the whole space from floor to roof may be zoned and populated.

The plants of a life-community in their quest for light may become differentiated in time as well as space. In the lower layers of most woods, for instance, there are a few shade-loving plants that can grow and flower even in the leafy summer when nine-tenths of the light or more is being intercepted by the crowns of the trees. But if the early bird catches the worm, the early plant catches the light. Accordingly, another and the more numerous section of this layer of the woodland-community is made of specialists in vernal growth, which shoot up into activity to catch the early sunshine of the year before the trees have time to spread their light-traps across it. The primroses and wood-

anemones and bluebells of English woods, the hepatica and the blood-roots and the spring beauty of the woods of America, all flower while there is still light in the lower storeys of the forest. Most of them are active for about three months of the year, and sleep away the rest.

In prairies and still more in deserts this seasonal specialization is very strongly in evidence, but it is concerned with water rather than light, of which latter necessity there is here more than enough for all. The studies of the Desert Laboratory at Tucson have shown how the desert plants divide up the year's rainfall of the Arizona desert. The first warmth of the year, combined with the slight winter rainfall, brings up a crop of small annuals, not markedly different from the small annuals of less extreme climates. They shoot up in January, flower in February, fruit in March or April, dry up and live through the rest of the year as seeds. And there is also a crop of perennials which have the same short period of active life, and survive the rest of the year as bulbs or leafless stems or underground root stocks. But as April passes, the temperature becomes very high and the rainfall declines. The tender vegetation dries up. This is the season of the plants we are accustomed to think of as most typical of deserts—the cactuses, the agaves, the yuccas. They can accumulate stores of water in their stems or leaves, and live and flower and fruit through the drought at the expense of these stores. They hold the stage until June is over. Then comes the main rainy season, with even higher temperatures, and the whole landscape changes marvellously. Millions upon millions of seedlings spring up and make the desert fertile. Speed is the keynote of their existence, for they must finish flowering and fruiting before, in less than three months' time, the next season of drought falls upon the land. And during this second drought, from late September on to the end of the year, with no rain and with increasing cold, the plant-life of the desert is almost at a standstill.

In the sea other seasonal factors come in. The researches

of Atkins have shown that the reason for the sudden drop in the abundance of surface life during the summer months is that the diatoms and other basic food-producers of the sea have exhausted the available phosphates in the surface waters. Not until after the winter, when cooled surface water sinks and phosphate-rich water rises from the unexhausted depths to take its place, can the full stream of life's abundance flow again.

When we pass from the fundamental vegetable hierarchy of a life-community to its animals we find a much greater amount of specialization and variety. We find not merely the herbivores that eat the plants, but the carnivores that eat the herbivores; we find parasites, a special and intimate sort of herbivore or carnivore, and we encounter scavengers which live upon the decaying remains of creatures of any possible grade in the scale. The scavengers of animal remains play a very different part from the scavengers of plant remains. The former (such as jackal or blow-fly grub, or the dung-beetle, though his actual food be vegetable remains extracted from the dung) are hangers-on of the purely animal part of the organization; they are exploiters of exploiters. But the scavengers of plant remains (such as the worms that eat dead leaves or the termites that eat dead wood) must be grouped together with parasitic plants like mistletoe and many fungi, and the few animal parasites of green plants, with the herbivores. They are all to be classed among primary exploiters of green plant activity, middlemen between green plants and other animals.

Of these intermediaries, every community will have a few basic kinds which are the foundation for most of the rest of the community's animal life. From the point of view of biological economics, they are the animal counterparts of the dominants among the plants; but they differ in being often (though by no means always) small and inconspicuous, their importance unrealized by the casual naturalist. The tiny copepods of the sea, the sap-sucking plant-lice, the earthworms of the soil, carry on such

decisive rôles, determining as they do the character of all the higher forms that prey upon them, quite as much as do such familiar herbivores as rabbits, sheep or deer.

The carnivores are usually organized in what are called food-chains, each link of the chain serving as food for the next. If we eat sheep, we eat plants at one remove; if we eat snipe or woodcock, we are eating them at two removes, with worms and such small creatures making another link in the chain. Parasites, too, may be organized in chains, parasite upon parasite, "little flea" upon "big flea."

Again, each of the main groups of exploiters, herbivores, carnivores and the rest, can be subdivided into well-marked minor rôles, which will be found, played by one actor here and another actor there, in all well-developed life-communities. There is, for instance, the rôle, whose importance in biological economics is not very commonly suspected, filled by the suckers of plant juices. This rôle is almost always undertaken by insects, almost all of them small insects—plant-lice, coccids, plant-bugs and the like—but the sum total of their pumpings is enormous, and converts a vast bulk of plant substance into a condensed animal form which then becomes available to carnivorous insects like ladybirds, and so passes, directly or indirectly, to bigger animals such as birds and mammals. All these higher forms are obviously conditioned by these juice-suckers.

Among the carnivores, there are carnivorous insect-eaters, some of them insects themselves, with spiders, too, and frogs, reptiles, birds and mammals. These insect-eaters fall into many sub-groups. There are the hawkers of flying insect prey, such as dragon-flies, swallows, swifts, nightjars and some hawks, the ant and termite specialists like ant-thrush and flicker, ant-eater and ant-bear, the devourers of wood-boring types, such as the woodpeckers and other birds, the pickers-off of parasites like the tick-birds, and so forth. And then in a grade above the insect-eaters, and conditioned by the insect-eaters just as these latter are conditioned by the insects, are the carnivores that

go for bigger prey, the hawks and owls, stoats and cats, wolves and boa-constrictors.

Among the scavengers there are the eaters of dead and decaying plant remains, like earthworms; the hangers-on of bigger carnivores, like the proverbial jackals with the lion; the undertakers of small corpses, like the burying-beetles; the funeral specialists of larger creatures, like vultures and marabou storks; and the devourers of dung, like the sacred scarab.

This life-drama, we have seen, is stereotyped in plot and construction, with the same main rôles to fill wherever it is played. But the cast varies. A rôle is played here by one kind of organism, there by another. It is interesting to note a few examples of how the actors fit themselves to their parts, how the same niche is filled in slightly different ways.

What we may call the earthworm rôle, the soil-making rôle, is filled in arctic regions like Spitsbergen by hordes of the tiny insects called Collembola or spring-tails; in tropical forests it is partly filled by termites. On various coral islands it is filled by land-crabs; the most important source of humus there is rotting coco-nut husks, and these the land-crabs burrow into and consume, much as earthworms burrow into soil and consume the most important source of humus in temperate countries, decaying leaves.

Wherever there is abundance of sedentary and edible food, whether it be plant or animal, there is a rôle to be filled by browsers. Sea-slugs and sea-snails browse on sea-weeds, and many coral-reef fish browse on coral, just as land-animals like rabbits and sheep and deer browse on grass and bushes. Carnivores often take to supplementary diets and to scavenging. In Africa, the spotted hyena lives largely on the remains of lions' kills; in the high north, the arctic fox is kept alive in the winter by the remains of seals killed by polar bears. The resemblance goes farther, for the arctic fox supplements his diet with sea-birds' eggs, the hyena with the eggs of ostriches.

The pursuit of earthworms in the soil is undertaken in

Europe and North America by the common moles; in Africa by the quite separate family of golden moles, and in Australia by the pouched moles—marsupials, not placentals at all; and there are some rodents which have taken to a not dissimilar life.

These examples show how the plan of very different communities tends to repeat itself even in the details of its arrangement. Manifestly a life-community is an organization, with a definite unity, an individuality of its own for the exploitation of natural resources.

Different kinds of plants and animals do not occur together haphazard; they are sifted out, selected, mutually adapted until a working organization results. Thus the life-community, if not an organism, is an organization of species which fill definite rôles, just as the body is an organization of parts and organs each with its special function. Certain kinds of species must be there for the life-community to live, just as certain kinds of organ must be there for the body to live. The life-community must have first its manufacturing side, the green plants; the different members of this department will be specialized to utilize light, air and moisture to the fullest extent, the dominant kinds doing most of the work, but the others subsisting either upon the surplus of raw materials left over by the dominants, or getting their chance during parts of the year when the dominants are inactive. Then when the raw material has been lifted to the organic level, a new series of forms, the animals and parasitic plants, play their part. Though animals do none of the primary production and are not self-supporting, yet in them life attains its most varied forms and its greatest intensity. They are arranged in successive grades. There are first the more basic grades which attack plants or their remains directly. These in their turn give sustenance to others—carnivores, parasites and the scavengers of animal corpses—which radiate out in linked chains from the basic plant-consumers. All these must be present in sufficient quantity and vigour if the life-

community as a whole is to carry on its rhythms without catastrophic change.

§ 4

The Growth and Development of Life-communities

Whether by Nature's agency or man's, bare stretches of land, devoid of life, are sometimes produced in the middle of fertile regions. A forest fire leaves nothing but dead trunks and charred soil behind it; on the shores of seas and great lakes, the wind and the waves may pile up great ranges of barren sand-dunes; a landslip or a rock-slide may strip a mountain-side of vegetation; mining or drainage or reclamation projects may leave big patches of untenanted soil.

These stripped areas do not stay bare. Life invades them again, and the invasion is a regular and orderly affair. There is a progression of inhabitants, one set of animals and plants succeeding another in sequence, until finally a stable state is reached. In a state of nature, the animal and plant life of this stable phase is the same as the original life on the area. The life-community has reproduced itself.

This community-reproduction was seen on the grand scale after the great eruption of the volcano Krakatoa, in the East Indies, in 1883. In three terrific August days the island blew itself in half, and threw such vast quantities of fine dust (more than four cubic miles of it) into the air that it floated round the world and for many months coloured European sunsets a richer red. On the island itself, and the two smaller neighbouring islands, Lang and Verlaten, every vestige of life was destroyed. The nearest land from which life could come was another pair of small islands about fifteen miles off, but they themselves had been three-parts devastated by the eruption. Java and Sumatra lay each about ten miles farther distant.

Less than three years after the explosion, a Dutch botanist visited the island. The ashy soil, from sea-level to peak, had been covered with a gelatinous layer of blue-green algæ mixed with diatoms and bacteria, in which a number of mosses and eleven kinds of ferns were growing, some of them abundantly. These had all been brought by the wind in the form of tiny spores. In addition, there had appeared a few species of flowering plants, some from wind-borne seeds, some from seed floated in to shore by ocean currents. The ferns and the flowering plants were all growing as isolated scattered individuals, and there were no shrubs or trees.

Ten years later, a second visit showed the flowering plants in the ascendant: fifty species of them had arrived. In various places the ferns and flowering plants had closed their ranks to cover the soil. Inland were stretches of a regular jungle of tall grasses; and along the shore a characteristic community of straggling beach plants. Shrubs were scattered here and there, and a few rare trees had taken root. But there was no indication of anything that could be called forest.

Finally, in 1906, twenty-three years after the eruption, a party headed by Professor Ernst visited the islands. They were now the home of a rich vegetation. All along the shores a strand-forest had grown up, with several kinds of figs, and abundant coco-nut-palms, many of them with ripe fruit; and there were patches of a different kind of forest here and there in the ravines of the interior. Over ninety kinds of flowering plants and fifteen of ferns were discovered; and not only were there abundant mosquitoes, ants, wasps, birds and fruit-bats, but lizards had reached the island, including a three-foot monitor.

In spite of its luxuriance, the plant-life had not yet developed into a series of typical communities, each with its own few dominant species. New species were still arriving, and many kinds of plants to be found on neighbouring islands had not yet reached Krakatoa.

Ernst estimated that it would take another half-century before the full richness of tropical climax vegetation had reproduced itself on the island; but considering the total annihilation of life, and the island's isolation, the progress made in twenty years is remarkable enough.

The lowest type of plants, wind-borne as minute germs, were needed to prepare the island soil, save round the level shores. This first primitive community paved the way for mosses and ferns. Each new addition helped to stabilize the soil and made it easier for higher plants to germinate; and so herbs and grasses, shrubs, and finally trees, came in in their due order. It would be difficult to find a more striking example of long-range colonization and slow successional development.

After the grand, the little. The same colonization, the same succession, will be seen in a half-pint of boiled hay infusion. First come bacteria, their ubiquitous spores settling into the liquid from the air. Then, once these have turned the organic matter of the hay into food fit for animals, there appear tiny infusorians like Paramecium, and finally predaceous protozoa that eat their vegetarian brothers as tigers eat deer. This succession has no permanency about it; it is living on the food-substances put into the water by man, and all the teeming life comes to an end in starvation, death and decay, unless green plants (in the form of single-celled algæ) manage to gain a foothold. This they can only do at a particular stage; but if they succeed, they pave the way for a new phase of development, with quite different sets of inhabitants, which finally leads up to a balanced, self-supporting community of microscopic plants and animals.

Recolonization like that of Krakatoa is seen whenever a jungle clearing is left to itself, though here the reproduction is partial and regenerative, not complete, since by no means all the normal life of the area is destroyed, and only the later stages of the community's development have to be reformed. In some parts of the tropics, the people clear and

cultivate patches of forest for a few years, and then, when the soil's fertility is exhausted, move on to new regions. In a brief space, the clearings are swallowed up again, silently and inexorably, by the primeval jungle. Air-photographs show various stages in the process. In one place, a few trees are invading the edges of the clearing like dots of mould on a piece of bread; in another, a clearing is half devoured; in yet another, it is covered entirely, but the forest has not yet assumed its normal character; the full typical rain-forest eventually resumes its sway as if man and his works had never been.

The speed with which development of this sort proceeds, especially in its early stages, is truly remarkable. Let us take a recent example. During the War, the sea was deliberately let in over large stretches of Belgian land near the River Yser (including some of the richest agricultural land in the country), in order to prevent the German advance. By the time peace came every land-plant had been killed off, and the sea-life had made great progress in taking over the territory thus made available for it. But in 1918 the land was drained again, and the lost district restored to land-life. The wet soil began to dry; meanwhile, salt-marsh plants colonized it and helped to loosen it with their roots and to fertilize it with their dead bodies. Only a year later most of it was covered with a rich crop of grasses, asters and other plants, and after three years only the skeleton shells of barnacles and mussels here and there on fences and posts made it possible to believe that the whole countryside had so recently been covered by the sea.

The actual steps by which the normal world of life is re-established have been carefully worked out in a great many cases, and we know now almost as much about the details of ecological succession as we do about the development of individual plants or animals. Those who are interested in the subject can pursue it in such books as Tansley's *Types of British Vegetation* or McDougall's *Plant*

Ecology. We must confine ourselves to a few illuminating instances.

Here and there on the shores of the Great Lakes of North America, the accumulation of dry sand provides bare areas for life to colonize. How it does so has been carefully studied on the Indiana shores of Lake Michigan. Sand brought by the waves dries in the sun, and its surface layer is blown off by the wind. Great strips of white lifeless sand accumulate, and may be heaped up to form dunes, dry on the surface but moist below. Only a few exceptional plants can colonize such an area; they must be able to do with a miserably low allowance of the mineral ingredients needed for plant growth; and they must be perennials and able to bind the sand with their roots so as to prevent the dune moving slowly along with the prevailing wind, and overwhelming its plant inhabitants in its march. The sand-grass Ammophila and the wormwood are among the few plants that can manage this. Sometimes the dune grows too fast and runs away from their control, and all the pioneers are overwhelmed. But they may keep their home fixed: then other grasses and plants like the wild rocket are able to come in and thrive now that the original deficiencies of the sand have been to some extent corrected by manuring with the decayed leaves and roots of the pioneers. After them, bushes like junipers and sloes can get a footing.

When dunes get out of hand, their movement gradually slows down as they get farther from the windswept lake shore, and as soon as it drops below a certain speed they are "captured" and immobilized by plants, the capture usually proceeding up from the base of the sheltered lee-slopes. The capture of dry dunes is effected by the same sand-grass and wormwood series of plants which we have just mentioned; but where there are damp depressions in the sea of dunes, the pioneers are rushes, willows and cottonwoods.

Eventually, however, the dry parts of the dunes grow

moister, and the wet depressions grow drier, as plants live and die in them; the pioneer vegetation then gives place to another set of plants—Solomon's seal, horsemint, goldenrod and other familiar flowering plants, with shrubs like dogwood and bearberry, and soon a few pine-trees. The soil is now rich enough for more exigent kinds of trees, often black oaks. New shrubs and herbs follow the trees; the soil grows richer. Red oaks succeed the black oaks and, finally, when a thick layer of humus has been formed over the dune, sugar-maple and beech gradually replace the oak, and persist indefinitely, unless man interferes. And, of course, each stage in plant-succession has its own animal inhabitants.

When the first white men came to Indiana they found this beech-maple forest in possession of the country wherever conditions were favourable. It was the fullest final expression of vegetable life in the region. To-day we see this same life-community reproduce itself, in the space of a few score years, by the conquest of new-formed and barren land.

In this story there are two or three points of special interest. The first and most fundamental is that each life-community is something which develops. What we have been talking about hitherto are for the most part only the final stages of development, called *climax* stages by ecologists, and corresponding closely enough with the adult phase of an individual's life. But for a climax phase, such as a forest or a prairie, to come into being, it must have passed through a whole series of developmental stages. And just as in an individual, reproduction must be by simple structures like egg or spore or gemmule, whose development into the adult stage is through steps of increasing complication, so the pioneer group of organisms by which alone the life-community can reproduce itself is much simpler than the climax phase. It contains many fewer species; they are never big like trees, and are often, indeed, very small; and they make few demands upon Nature and so can get on in spite of poor soil.

In the developing single organism, each phase is its own executioner, and itself brings a new phase into existence, as when the tadpole grows the thyroid gland which is destined to make the tadpole stage pass away in favour of the miniature frog. And in the developing community of organisms, the same thing happens—each stage alters its own environment, for it changes and almost invariably enriches the soil in which it lives; and thus it eventually brings itself to an end, by making it possible for new kinds of plants with greater demands in the way of mineral salts or other riches of the soil to flourish there. Accordingly bigger and more exigent plants gradually supplant the early pioneers, until a final balance is reached, the ultimate possibility for that climate.

Another point is that, whether the sand was colonized when it was too dry or too wet for most plants, the eventual result was the same—beech and maple forest. This is but an example of a general rule—that the general course of community-development makes dry environments moister, and moist environments drier. Even where development starts in the water, it is headed towards forest or whatever the normal climax of the region may be; for water-plants are all the time choking up their watery homes. We have already given an account of the zones of vegetation that characterize a large pond—floating plants, often microscopic, in the centre; then wholly submerged plants like pond-weeds; then plants like water-lilies and water-crowfoot, that send their leaves and flowers up to float on the surface; then the plants that, as it were, merely wade or paddle with their feet in the water—bulrushes, arrowheads or pickerel weeds; and often a marshy zone with sedges and irises making transition to the real dry land. The plants grow and die, their remains accumulate, they help to silt up the pond. Thus, the water shallows, and the zones move in towards the centre. Presently the central zone is crowded out altogether, then, in the course of a few years, or scores of years, the next, and so on—unless man

interferes—until the whole pond has become dry land, at first wet, then drier, and eventually fit for trees to grow on.

We have already seen that the most unpromising dunes of bare, dry sand are made progressively richer and wetter by the accumulation of humus, until they too will grow trees. The same is true even of bare rock. Lichens are here the pioneers—first the ones like thin crusts, and then, when these have disintegrated the surface a little, the leafier ones, together with a few mosses. These plants catch a little dust and debris and so start the rudiments of a soil. Other mosses now come in, and a few grasses; and flowering herbs soon follow. Each addition to the population accelerates the rock's disintegration and helps in forming soil. Bigger herbs like golden-rod and shrubs like blackberries can now invade the place, and eventually the coating of humus is thick enough for tree-seedlings to take root. And so a rich woodland takes the place of dry, bare rock-surface.

The way in which quite different developments from wet and dry beginnings may converge to produce the same adult phase is well shown in some of the middle-western States, such as Indiana, where all vegetation is destroyed in the process of surface coal-mining. The mining operations convert the area into a series of ridges and furrows, the ridges anything up to thirty or even forty feet high; and these bare "strip-lands" are usually left to themselves. The bottom of the furrows are wet, and may contain standing water; the tops of the ridges are drier than the neighbouring country. Although the wet furrows begin their development with bulrushes and water-plantain and cocklebur, and the dry ridges with white melilot and asters, sunflowers and ragweed, both will end up, often in the short space of twenty-five years, in woodland typical for the region, consisting mainly of sycamore, elm and honey-locust.

Many other examples could be given; but the principles remain the same. Life-communities develop; they de-

velop from slight beginnings, and become progressively richer because each set of invaders paves the way for another, which grows more richly because it makes greater demands on the soil. And however they begin, they tend in any one region towards the same stable climax.

This stable climax may not always be reached. It is the potential end which the climate of the region permits to its life-communities. But other factors may step in and prevent the potentiality from being realized. Though a pond will silt up in a comparatively few years, a lake may take immeasurably longer. Steep slopes and unfavourable soils, too, will retard or prevent the appearance of the climax stage, as absence of iodine in water will prevent newt-tadpoles from turning into newts. Perhaps most important of all, animals in general and man in particular may prevent the normal climax from appearing. In a later section we shall see how rabbits may turn woodlands into close-cropped grass-heath. Darwin found that cattle, by eating down the seedlings, prevented the heather commons of Southern England from achieving what ought to be their last stage in development and becoming pine-woods. And it seems almost certain that the lovely close turf of the English chalk downs is not Nature's climax, but a substitute, induced by man's clearings, and his sheep's croppings, for the more natural final phase of beech-forest.

We have spoken mainly of plants in this section. This is because animals usually follow the lead of plants. Plants must be the pioneers in exploiting the environment; and the final climax generally takes its main character from the plants which succeed in becoming dominant. One has only to think of the difference between a pine-wood, a prairie and a peat-bog. The animals of a community are not only dependent upon the plants for food, but their whole existence is modified by the character of the vegetation. It is hardly too much to say that while the effective environment of plants is provided by inorganic nature, the effective environment of animals is provided by plants.

An equatorial rain-forest owes its very existence to the intense light and heavy rain of the tropics. But the animals which live in its shelter receive very little light—less, indeed, than those of the arctic tundra; and though the air is damp, there is often a shortage of liquid water. It carries a special climate within itself. Furthermore, the forest provides a special mechanical environment. It encourages animals which can climb and swing from branch to branch, while the prairie and the pampas encourage burrowers and hoppers.

In the sea, where the main store of plant-life is floating and microscopic, and animals often fixed and plant-like in their growth, this primary importance of trees and vegetation does not hold; in coral reefs, for instance, the main lines of development are based upon the succession of different kinds of corals, and the character of the whole community is given by the coral-climax, which provides effective environment not only for other animals, but for many seaweeds, large and small.

The facts of succession help to make clear a point of some general interest. The biologist is often asked why primitive types survive alongside of those that are more advanced, why they did not also evolve. The answer is really clear enough. During the course of evolution the more advanced types came into being in a world prepared by the life that had gone before. But they still need that preparation. They can only be large, strong, efficient, by making great demands upon their environment—the higher plants upon the soil, the higher animals directly or indirectly upon the higher plants. A tree cannot grow on bare rock, nor a sheep subsist on blue-green algæ. Many of the primitive forms of life survive by taking advantage of the less favourable kinds of environment that are always being brought into existence. Their own activity paves the way for their own supersession by higher types; but meanwhile their ubiquitous spores and germs have colonized other poor environments. Life exists by exploiting its environment. Competition forces a division of labour upon it. The

environment is most fully exploited when each nook and aspect is worked by its own particular kind of life. And so, besides creatures adapted to secure the riches of Nature in the most specialized and efficient ways, we should expect to find types which are adapted to her poverty—to barren and out-of-the-way environments like caves, to unconsidered nooks and crannies in rich environments, to times and seasons when the dominant plants are not at work, and to temporary opportunities in the environment, such as those we have been describing, when the feeble can thrive but the powerful not yet. And on the whole the creatures adapted to these poor holes and corners of space and time are creatures of primitive type.

Another fact of succession has some practical importance. In general, the natural vegetation of a region is the most luxuriant that it can support. There are exceptions on oceanic islands, because they may never have received the best complement of plants. There are also exceptions due to the fact that Nature has hitherto not produced the most efficient kind of plant for the environment. The Lower Devonian lands had no forests because no trees had yet been evolved. This sort of thing may still happen. Of recent years, a remarkable grass has appeared which can grow on the fresh mud-flats of estuaries and harbours and cover them with rich vegetation. Hitherto such mud-flats have remained bare.

The grass in question is called the rice-grass, *Spartina townsendii*. It appears to be a natural hybrid between a native European species and one brought accidentally to Europe from America about a hundred years ago. However produced, it spread, slowly but steadily, from bay to bay and estuary to estuary, converting mud into meadow. The botanically remarkable fact about it is that it takes the ground it covers to an ecologically higher stage of development. As Professor F. W. Oliver says: "These bottomless muds, though they stood empty of vegetation and invited colonization, probably for thousands of years, found no plant capable

of solving the problems of invasion and establishment till *Spartina townsendii* came and made light of the task." And the practically remarkable fact about it is that it provides the only case known of a plant which spreads rapidly and is not a pest, but a benefit, to man—up to the present at least, for it is on the cards that it will eventually begin to choke up harbours.

In the first place, it makes new land, and, in the second, it provides a valuable crop. Round its plants the level is raised, and in place of mud, in which men may get bogged and even disappear, firm saltings develop. In place of a bare surface there grow fields of tall green grass, three feet or more in height, eagerly sought after by all stock and capable of being made into excellent hay. It may even prove possible to use it for paper-making.

The English, maritime and with no great land-hunger, do not particularly encourage it; but the Dutch are using it on a large scale for "poldering"—making new land by banking. Single slips are planted in the mud three metres apart. In three years the tufts have covered half the mud, in six years they all coalesce to make one meadow, with a surface about two feet above that of the original flat. *Spartina townsendii* will help Holland to accelerate very considerably her struggle to reclaim land from the sea.

Could man but find a plant which would do for fresh-water bogs what the rice-grass can do for seashore muds, enormous areas of land, especially in the tropics, could be quickly and cheaply made fertile. With the rice-grass before our eyes, we can go on experimenting with reasonable hope of success.

The rice-grass thus takes maritime muds to a new stage of development. This is an exceptional type of human interference in a life-community. In general, the normal wild state of affairs is the highest, and when man interferes with vegetation he usually keeps it from attaining its natural climax. The major part of temperate Europe and North America should by right of nature be forest; the great

stretches of grass and heath that exist there to-day owe their existence to man's activities in tree-felling and cultivation and in encouraging grazing animals. The grassland of the English shires is only waiting to become woodland again, but the grassland of the American prairies is grassland in its own right—the ground is not wet enough to develop naturally into forest. Only when man supplements nature, as when he irrigates the desert, does he carry the climax a stage higher than normal; and even then he may find the task harder than he imagined.

§ 5

The Grading of Life-communities

In the preceding section we have traced out the way in which a typical life-community develops from small beginnings up to the climax which is its normal completion. But in different regions the kinds of climax differ. In many parts of the world's land-surface the adult stage, so to speak, towards which all other arrangements of living things are tending, even if they are tending thither so slowly that they never actually reach it, is forest. In other words, the dominant plants of the climax are generally tall trees. Where the climate is not suitable for trees to dominate all smaller plants and form a forest, other types of climax occur; and in this way life is zoned over our planet's surface. The broadest zoning is the zoning by latitude. The normal climax of equatorial life is the typical rain-forest, green all the year round, with a multifariousness of splendid trees instead of one or a few dominant species. In monsoon districts, where rainfall is heavy but intermittent, the forests cease to be evergreen; they drop their leaves in the dry season. As we pass north and south towards the sub-tropics the amount of rain falls off, and the trees, unable to find sufficient moisture if they close their ranks, have to relinquish part of the soil to scrub and grasses. Dominance must be

shared between them, and the result is the beautiful climax we call savannah-forest, where clumps of trees are dotted about with broad spaces between, as in a park.

With increase of latitude, we enter the world's two desert belts. We come into a region not only of lesser heat, but, under existing geographical conditions, of desiccation. The trees grow sparser, smaller, thornier, often with tough leaves. The African thorn-scrub is of this zone. As regions of less and less rainfall are approached the vegetation finds it more and more difficult to suck up the moisture it needs, and eventually the small plants, obeying the same necessity which overtook the trees long before, are forced to break their ranks. No longer is the surface of the ground completely covered with vegetation. The life-community, in the language of ecologists, is no longer "closed," but "open"; the lack of moisture has become a limiting factor and prevents life from fully exploiting the other resources of the soil.

The desert often passes over into steppe-deserts, steppes, veldts, and bad-lands, where the rain—small in amount and falling mainly in winter—usually only suffices to support an open community of grasses and shrubby plants like wormwood and sage-brush. As we pass farther polewards we reach, as a general rule, wetter country again, and the open communities of the true steppes give place to the full grassland of the grass plains, the prairies and the pampas, where vegetation once more covers the earth. All gradations occur from the short-grass plains that are only just closed communities to the tall-grass prairies whose plants are bigger and have deep-penetrating root systems.

These grasslands, open and closed, are for the most part found inland. Near the coast in the same latitudes climate is rather different, and generally allows a different climax, a climax of scrub or even forest. The rain falls mainly in the winters, and the plants' growing season is dry. Accordingly the trees of such sub-tropical and warm-temperate forests are adapted to low rainfall by being evergreen and having tough, leathery leaves. The chaparral in Texas, the maquis

scrub and the forests of Aleppo pine and other conifers in various parts of the Mediterranean region, the Spanish woods of cork-oak and holm-oak, the forests of southern California and south-west Australia are examples. One of the tragedies of history is the cutting down of these warm-temperate forests over great areas of the Mediterranean basin, as in Dalmatia; green hillsides have given place to naked stony rock, perennial streams have turned into intermittent torrents, and the climate itself has been altered for the worse. In the last few years, however, a determined effort has been made to restore this coast to its pristine wooded state.

North and south of these dry, warm-temperate regions we come generally to a moister warm-temperate climate. Here deciduous trees like beech and oak, maple and ash, locust and chestnut, walnut and sycamore, are the usual dominants. Where soil is poorer, however, or rainfall less abundant, evergreen conifers can do better, and they give us pine forests such as those of Scots pine or Austrian pine in Europe, long-leaf and loblolly pine along so much of the south-eastern coastal plain of the United States.

Conifers reappear again polewards of the main temperate zone. They encircle the whole of the northern hemisphere. An almost unbroken belt of them, four hundred to eight hundred miles wide, stretches for over five thousand miles from Scandinavia to the Pacific. In Siberia it is called taiga; but elsewhere, strangely enough, it has earned no special name. And a second huge forest of the same type covers the North American continent from Labrador to Alaska. Sometimes such a forest is all of fir, dense and gloomy; but deciduous trees like birch and alder may break the inhospitable monotony. Firs, however, are the dominants. Yet this does not mean that they find themselves here in the most favourable conditions, for spruce from sub-arctic North America grows much larger and better when transplanted to the milder climate of Scotland. It only means that, in the

struggle for existence, they can survive where other trees with greater demands fail. They are not in any perfect adjustment with their not very attractive environment, but they are better adjusted than all other trees.

Towards the north (there is no corresponding belt in the south, owing to the disposition of land and sea) the forest thins out, just as the very different tropical forest thinned out towards the desert region. Trees can no longer grow where the subsoil is frozen all the year round; they dwindle, grow dwarfed and stunted, and eventually disappear, leaving only the arctic barren-grounds, with their permanently frozen subsoil, to which the name tundra is given. Dwarf and creeping willows, grasses and sedges, are the chief among the tundra's higher plants, though bright flowers are by no means absent, and saxifrages and buttercups, campions and pale yellow arctic poppies and many other lovely plants, often crouched on the soil in cushions and rosettes, star the sunnier places during the short two or three months' summer. Lower types of plants like mosses and lichens are here relatively more abundant than anywhere else in the world, and may actually dominate the tundra's more vigorous regions. The " Reindeer Moss," for instance, which is really a lichen, may extend almost unbroken over great regions of the American barren-grounds, often growing six inches or a foot high.

And finally, before life is made wholly impossible by perennial snow-fields and ice-caps, cold does what drought did in the desert belt: it breaks the closed ranks of the plants. When conditions become too extreme it is only here and there that plants can grow at all—where a slope faces south, where a patch of good soil has managed to accumulate, where snow is off the ground long enough for plant-life to run a segment of its course. Between the tundra and the ice-fields in Greenland and other arctic regions there may be such a zone, with a few poor plants in a desert of stones; and the antarctic continent nowhere knows any richer vegetation than this.

We have so far spoken of the zones of life on land alone. This is not because the grading of life is less important in the sea, but because we know less about it. We know that floating life is in general less abundant in warm waters than in cold, owing largely to high temperature reducing the amount of carbon dioxide in solution in the surface waters. But recently, thanks largely to the invention by Professor A. C. Hardy of an automatic plankton-recorder—an instrument which can be towed through the sea behind a ship, and which traps and preserves all the little floating organisms in its path and rolls them up neatly in order on a scroll of gauze for the investigator to examine at his leisure—we are making a beginning with a quantitative mapping of the sea's vegetation. A century hence the maps of the world will in all probability have diatom-belts marked on all the seas as they now have vegetation-belts marked on the lands; and a knowledge of these will be of great help to fishermen, and to whalers—if human improvidence and the absence of a cosmopolitan control of the sea have by that time left any whales.

This is grading on the grand or planetary scale. But there are other kinds of gradients. Altitude, for instance, proves a very good substitute for latitude. We can start at the equator in the Congo rain-forest, and by the vertical ascent of less than three miles to the peak of Ruwenzori, reach the same lifeless cap of snow and ice that we should have had to travel more than five thousand horizontal miles northward to find in the mountains of Spitsbergen. And in our ascent we should have passed through belts of vegetation almost as diverse as in that long, horizontal poleward stretch. Above the tropical forest, park-like savannah-forest, with richer, greener vegetation in the stream-gorges; and here and there bare and grassy stretches, treeless. Then, as the cool and the mountain rains begin, a queer forest of tree-heathers, all festooned with hanging moss. Above that, again, a still queerer forest of groundsels and lobelias grown to the stature of trees, looking not like any familiar terrestrial trees, but

trees produced by some other planet. This gives place to mountain meadow and this gradually to a true alpine flora, nestling in isolated tufts among the rocks. And above this, rocks and ice and snow untouched by life.

Gradients in moisture may occur within a single climatic region, according to the lie of the land. There is such a gradient from every marsh or pond to the solid land around it, in every valley from the moist bottom up to the drier slopes. In the margins of salt lakes there is a gradient in salt-content of the soil, just as there is in salt-content of water between sea, estuary and river, or, in some inland seas like the Baltic, between one end of the sea and the other. There is a gradient in the amount of sunlight as we pass round the shoulder of a hill from south to north aspect, or as we pass down from shore-level to deeper water in lakes and oceans. And there are other gradients in the environment—gradients in amount of oxygen dissolved in water, in acidity or alkalinity of soil, and so forth.

Each and all of these minor graded changes in the environment are reflected in its living inhabitants, just as definitely as the vaster change between equator and pole. And the change is always reflected in the same way—by a gradation of life-communities. Round the shores of the Great Salt Lake, for instance, there is first a barren flat, too salt for any plant; then a zone of one species of glasswort, capable of tolerating two and a half per cent. of salt in the soil, then of another, more luxuriant species. Two or three further zones of shrubbier plants follow, until at a sufficient distance from the lake for the salt-content to have fallen to about one-tenth of one per cent., sage-brush becomes luxuriant.

The most familiar examples of such gradations are that between water and dry land on the seashore or round the margins of a shallow lake or pond. In every case, whether each grade extends for several hundred miles, like the prairie, or for a few feet, like the belt of bulrush round a pond, a striking fact is to be noticed. However gradually and continuously the environment may

change, the change in life is always more or less abrupt. Each belt of life is on the whole uniform, often remarkably uniform for most of its extent, and then in a short distance it makes a sudden transition to another and often markedly different belt. The cause of this is competition. If one kind of plant can do better than others in reaching up to the light, it will succeed, and the others will fail. This is why in each community there are one or a few dominant kinds of plants. Success in this kind of competition leads to dominance; but failure means not mere subordination, but complete or almost complete banishment. As long as the dominant species can hold their own, they can dominate. But when conditions change a shade further, they must give place to other and altogether different kinds of dominants. That is why there is generally such an abrupt change from woodland to prairie, or from one kind of seaweed to another on the seashore, why marsh-plants give place so suddenly to the bulrush zone round a pond, and why the timber-line is so sharply marked on a mountain. And in this way, since animals follow the vegetation, the rivalries of plants translate the sloping gradient of the lifeless environment into a staircase of life-communities.

Thus, with sufficient knowledge and patience, we could make a map of the whole world showing the distribution of life-communities as it was at a particular instant. But, as we were at pains to point out in the last section, it is not enough to think of life-communities in this fixed and static way, for they are continually changing. For one thing, they themselves are often reacting on their own environment, and so bringing about that community-development we call succession, up to the climax which is in equilibrium with itself. And for another, the environment itself is changing. Sea and land shift their boundaries; erosion levels mountains and builds plains; the belts of temperature move slowly up and down over the earth's surface as a glacial period or a dry spell comes and goes; and with such changes the life-communities must shift their boundaries too.

As Elton says:

> If it were possible for an ecologist to go up in a balloon, and stay there for several hundred years quietly observing the countryside below him, he would no doubt notice a number of curious things before he died, but above all he would notice that the life-communities appeared to be moving about slowly and deliberately in different directions. The plants round the edges of ponds would be seen marching inwards towards the centre until no trace was left of what had once been pieces of standing water in a field. Woods might be seen advancing over grassland or heaths, always preceded by a vanguard of shrubs and smaller trees; or in other places they might be retreating, and he might see even from that height a faint brown scar marking the warren inhabited by the rabbits which were bringing this about.

If he stayed up long enough and reflected sufficiently hard on what he saw, he would begin to draw some interesting conclusions. He would realize, for one thing, that the transition from one life-community to another in space usually corresponded to an actual replacement of one by the other in time. The mapping of the gradation of life-communities gives a spatial picture of succession. That is clear enough with the belts of vegetation round a pond; they move inwards, each one replacing its more central neighbour, until all but the outermost, now spread over the whole area, have disappeared. And he would realize that there is no essential difference whatsoever between the narrow rings of life round a pond and the broad rings of life round the globe. They both depend on gradients in outer conditions. The sole difference is this. The one is not merely a gradient on a small scale, but one which natural forces, both those of life and those of lifeless matter, tend to roll out flat; the other, however, is not merely on a large scale, but is determined by agencies outside the scope of any changes in itself—by the very shape of the world. The one is essentially temporary, the other essentially permanent. Even so, the succession of stages round the pond may be interrupted and set back, as when a succession of wet years floods the margins and reverses the normal development. And if you

like, you can think of equatorial forest as the climax community of the planet as a whole, towards which the life of all other regions is disposed to tend, though checked in its approach by limitations of warmth, of water, or of soil.

If our ecological observer could have stayed aloft during a geological period or two at the beginning of the Mesozoic Era, from the cold dry beginnings in the early Trias to the warm moist uniformity of the late Jurassic, he would have witnessed the world's life-zones narrowing inwards round the poles, just as the bordering plants round the pond encroach upon the water; and he might have been pardoned if he had thought that the process would continue until the whole world, poles and all, was one climax forest.

However, there must always remain a sufficient difference between pole and equator to keep life zoned by latitude; and there must always remain land, high and low, and sea, shallow and deep, to maintain the complex set of gradients which arranges life in a series of belts, from mountain to plain, across the sharp transition of the shore and down more slowly again to the abyss. These two gradients are permanent features of our world; all the rest are temporary, and tend sooner or later to obliterate themselves.

There is another way in which the little mirrors the big. The same competition which results in the comparatively speedy development of ecological succession results also in the portentous slow development of evolutionary succession. A landslip or man's destructive hand uncovers a patch of the bare earth, or impounds a body of barren fluid; it is colonized by a succession of communities, and in a few decades is tenanted with rich life again. The whole world, both land and sea, was once free of life; and æons later all the land was still one great bare patch of earth and rock. First the seas, and then the lands were colonized. In both there has been a succession of faunas and floras, each one on the whole exploiting the environment a little more effectively than the one before. Evolution is a slow succession of a series of ever new and ever improved communities towards

a still unrealized climax. The most up-to-date of life's existing communities are still very wasteful in their exploitation of the world's resources. It remains to be seen whether man, with his deliberate aim at a higher efficiency, his replacement of the hitherto dominant tree by his own cultivations and devices, will make a mess of things and fail, or will succeed and hold on from climax to climax. If he fails, the forest will return.

§ 6

Food-chains and Parasite-chains

Now that we have discussed the development and distribution of life communities, we can return to the details of their interplay. Green plants draw their supplies from lifeless and universal sources; animals must live on other life. So it comes about that different kinds of animals will be at different removes from the prime source of food; and one of the characteristics of the animal part of every community will be its organization in the form of subsistence-chains. A subsistence-chain is a series of creatures, each living on its predecessor in the series. There are two main kinds of them, food-chains in the ordinary sense, in which the predecessor is devoured, and parasite-chains; and of course there may be subsistence-chains of mixed type, of which both devourers and parasites are members. The general rule is for the members of food-chains to get bigger and bigger as they get farther from the chain's original starting-point, while in parasite-chains we find the opposite tendency—each link is likely to be smaller than the one before.

The starting-point of a food-chain is normally among green plants, but from one and the same starting-point many food-chains may radiate out in different directions. In an English wood, for instance, plant-lice suck the juices of the twigs; these, either before or after having fallen a prey to

spiders, are eaten by small birds like tits and warblers, and these in their turn by hawks. The same trees may contribute to the hawk's upkeep in another way. They drop their leaves upon the ground, the leaves are eaten by earthworms, the earthworms by blackbirds scratching among the underbrush, and the blackbirds by hawks. A different line is started through the seeds of the trees. Acorns and beechnuts are nibbled by mice, and the mice are the chief support of tawny owls; and there are other chains running through woody branches or stem, to wood-boring insects and woodpeckers, through seeds and squirrels, through leaves and caterpillars or gall-insects, and so forth.

In the sea, where the single-celled diatoms are the main food-producers, the first link in the animal food-chain is invariably supplied by tiny creatures, very largely the little crustacea we call copepods, but also the microscopic larvæ of many larger animals like crabs and sea-snails and starfish. These are generally the prey of little jellyfish, arrow-worms and small carnivorous fish, which in their turn usually fall victim to bigger fish.

A carnivore can only cope with prey within certain limits of size. Animals above a certain upper limit it is not strong enough to tackle; the most powerful spider cannot kill rabbits. Animals below a certain lower limit it cannot economically make a living off: a lion could not live, like a cat, by catching mice, nor an ostrich off insects as small as those that satisfy a tom-tit or a swallow. It is for this simple reason that each link in a food-chain is usually bigger, but not enormously bigger, than the one before. There are exceptions. The food-chain from the diatoms of arctic seas which passes through tiny crustacea, free-swimming pteropod snails, and fish may end in the body of a gull. But it may have a further link tacked on to it; this is the skua or jaeger which, though actually lighter than the gull, pursues and terrorizes it until by mere bluff and pertinacity it forces its victim to disgorge its last meal.

The skua, however (save for some depredations on eggs

and young birds), is not strictly a carnivore, though it is a link in the food-chain. But stoats feed largely on rabbits, which are both much heavier and much speedier than they. This they do by paralysing them with fear, in some way which is as yet not fully explained; it seems, however, that it is the smell of the stoat which has this extraordinary effect upon the rabbit. Other exceptions are apparent only. Wolves are less than a quarter of the weight of the deer they kill; but they hunt in packs, and the pack is the unit that counts. The extremist case of numbers thus making up for size is found in the driver ants; it needs hundreds of them to weigh an ounce; but their columns number millions, and they will eat anything, however much bigger than themselves, that cannot run away, from puppies and babies to tethered cattle.

The best example of an animal feeding on creatures vastly smaller than itself is the whalebone whale. It has skipped several links in the chain by means of its special sifting device; but even so its usual prey is about an inch long, and the first links escape it. All big current-feeders have similar devices for accumulating particles which would be no use to ordinary eaters of the same size; the outstanding case is Tridacna, the giant clam, which, in spite of living on microscopic debris, may grow a shell five feet across.

Not only is each animal link in a food-chain generally bigger in bulk than its predecessor; it is also much less abundant in number of individuals. For the carnivore can only live on the surplus production, so to speak, of the species on which it preys; and also it needs a huge bulk of material to keep itself alive. Percival, in his pleasant and informative book, *A Game-Ranger's Notebook*, tells us that one lion kills about fifty zebras every year. As this represents only one part of the surplus of zebras which must be produced to keep the numbers of the species constant, it is clear that the normal proportion of live zebras to live lions must be several hundred to one. Similarly, two American investigators who worked out the biological balance-sheet of Lake Mendota in

Wisconsin found that the single-celled plants which nourish the many-celled but still microscopic crustacea and wheel-animalcules that make the first animal link in the lake's food-chains, together weigh about fifteen times as much as the sum of their devourers. And in our previous example, a small wood might well shelter but one pair of hawks, dozens of tits and warblers, hundreds or thousands of spiders and millions of plant-lice.

The greatest number of links in such a food-chain seems to be five, and usually it is about three. As an example of a marine food-chain, and one of economic importance, we give that of the herring, worked out by A. C. Hardy. The diagram shows how the herring changes its food as it grows bigger. But it also shows how the starting-point always consists of single-celled plants, and the first animal-link almost wholly of one or another kind of copepod. And finally it shows what our readers may have been suspecting, that the various food-chains in a community need by no means be separate, but are linked up together in an interlacing meshwork like the chains in a coat of chain-mail (Fig. 24).

To work out all this web of interrelations in detail for a whole community is all but impossible, even in our temperate regions—let alone in the richer tropics—on account of the hundreds of kinds of animals and plants involved. To achieve anything like such completeness, the ecologist must turn to unkinder zones, such as the arctic, where the numbers of different species are so few that the food-cycle is reduced to a diagrammatic skeleton. Even such a skeleton, however, still has a considerable intricacy.

One or two interesting points in the integration of Spitsbergen life may be noted. There are no herbivorous mammals but several herbivorous birds. Otherwise fresh plants are eaten by midges and saw-flies, while the place of earthworms as the first animal link from dead plant-tissue is taken by the tiny wingless insects called Collembola, together with mites. All these tiny arthropods, before or after going through a spider link, are eaten by birds, and the birds are

eaten by arctic foxes. This store of fox-food, however, does not seem sufficient, and the hard-pressed carnivore is driven to supplement it by living at the expense of polar bears, either eating their dung or scavenging the remains of the seals they kill.

Another point is that the land is continually being enriched at the expense of the ocean. All the sea-birds—gulls, auks, guillemots and ducks—get some or all of their food from the surface stores of the arctic sea. Their dung, rich in nitrogen thus extracted from the ocean, manures the ground and helps plant-growth. Below one of the great bird-cliffs where (for protection from foxes) the nesting sea-birds congregate in thousands, plants that elsewhere grow as miserable stunted things, one or two inches high, shoot up to a foot, the whole aspect of the vegetation is changed, and one may fancy oneself back in a temperate country.

Parasite-chains usually link secondarily on to some animal in a food-chain, though there are abundant examples which take origin directly in plants, such as the insects which cause and inhabit oak-apples, robins' pincushions and other plant-galls, or the trypanosomes—single-celled protozoa rather like the ones that cause African sleeping-sickness—that live in the milky juices of plants such as spurges.

As a matter of fact, the majority of parasites are not linked up ecologically into chains at all; or, if we like to put it so, most parasite-chains have but one link. There are no parasites living on tapeworms or on malaria germs. But sometimes there are parasites of parasites; and then the parasite-chain is a reality.

In such cases the size of each link diminishes rapidly instead of increasing, as in the ordinary food-chain. Everyone knows Swift's lines:

> So, naturalists observe, a flea
> Has smaller fleas that on him prey;
> And these have smaller still to bite 'em
> And so proceed *ad infinitum*.

This is, however, an obvious impossibility, since a few

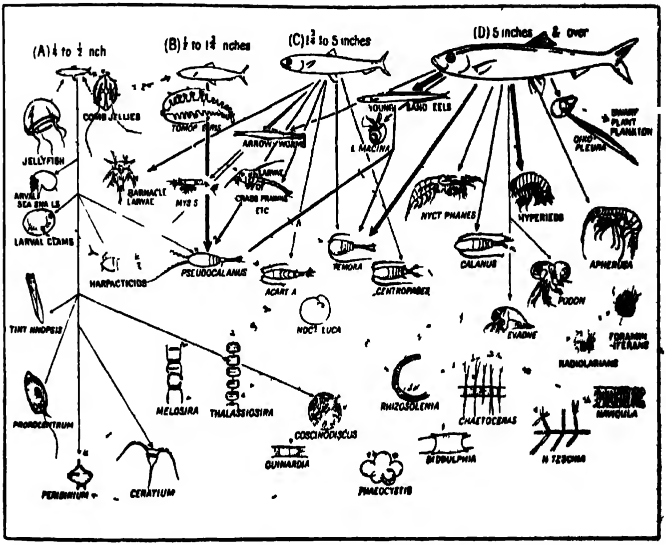

FIG. 24—A PICTURE OF THE FOOD-RELATIONS OF THE HERRING AT DIFFERENT STAGES OF ITS LIFE-HISTORY.

The solid lines point to food eaten directly by herrings; other links in the food-chains are dotted. (A) The young herring feeds mainly on single-celled plants, nauplii and mollusc larvæ, and small copepod crustaceans. It is eaten by jelly-fish, comb-jellies, arrow-worms and bristle-worms (Tomopteris). (B) During its next stage it lives almost entirely on small copepods and no longer takes any plants or small larvæ. It is still eaten by jelly-fish and comb-jellies, but not by worms. (C) From 1¾ to 5 inches, its diet is exclusively crustacean but more varied—several kinds of copepods and large crustacean larvæ, and Mysis. (D) From 5 inches and upwards it eats copepods, large crustaceans, the tunicate Oikopleura, pelagic snails and large numbers of sand-eels. The animals it eats support themselves either directly or at one remove on various single-celled organisms, mostly diatoms (Melosira, Thalassiosira, Guinardia, Chætoceras, Nitzschia, Navicula, Coscinodiscus, Rhizosolenia, Biddulphia), flagellates (Prorocentrum, Peridinium, Ceratium), and algæ (Phæocystis). (*Drawn from the data of Prof. A. C. Hardy.*)

links would bring us down to a size smaller than a single molecule; and, as a matter of fact, there seem never to be more than three or four links in such dwindling chains.

A two-link chain of sinister importance begins with the rat-flea and ends in the parasite which it harbours and may transmit to man—the bacillus of bubonic plague. In the same way parasite ticks have as secondary parasites the spirillum of relapsing fever. The secondary parasites may of course be quite harmless; the intestines of many kinds of fleas, for instance, teem with perfectly innocuous single-celled flagellates called Leptomonas. In all these cases, numbers go up when size goes down, as happens also in food-chains. A squirrel is quite likely to support hundreds of fleas, and each flea to shelter and nourish thousands of Leptomonas, though of course the total bulk of flea is only a tiny fraction of the bulk of squirrel, and the total bulk of flagellate again only a fraction of the bulk of flea.

Some of the most remarkable examples of parasite-chains are afforded by the parasitic hymenoptera, insects which, as we saw in our section on parasitism, can equally well be styled internal carnivores, their eggs, laid in the grubs or even the eggs of other insects, hatching out to maggots which consume their prey from within. Many kinds of these parasitic hymenoptera are themselves victimized by secondary parasites (sometimes styled hyper-parasites) belonging to the same group, and of the same unpleasing habits; and these in their turn may sometimes afford a livelihood to tertiary parasites of the same kind. Since each link may nourish parasitic protozoa in its intestines, the protozoa of the tertiary parasites make a fourth link; they are quaternary parasites. The insects which are tertiary parasites are all fabulously small.

Parasites and food-chains are sometimes tangled together in an interesting way. When one link in a food-chain is always being eaten by the carnivorous next link, any parasites that happen to be aboard are generally eaten, too; and so it is very frequent for parasites of a carnivore to become

adapted to pass part of their life-cycle in its prey, so as to make certain of reaching the carnivore's interiôr again when the time comes. So the tapeworm of the dog and fox has the rabbit for its secondary host, the trypanosomes parasitic in tsetse flies have become adapted, unfortunately for us, to living out part of their cycle in the blood of men and other large vertebrates, while Aggregata, a common protozoan parasite of squids and octopuses, divides its time between them and their favourite prey, crabs.

Sometimes there are three stations on the journey. The enormous broad tapeworm begins life by infecting a tiny fresh-water crustacean, passes on to a second stage inside a fresh-water fish when this eats the crustacean, and so on to a mammal like an otter, when it eats the fish. But there may be other effects. The food-chain is like a railway with one-way traffic; and parasites will always be moving down the line. Squirrel-fleas often hop off on to the squirrel's enemy, the pine-marten, and have been known to become more or less acclimatized to life in this new environment; most of them, however, seem to die here. Sometimes this transference has unfortunate results for mankind. When human beings take a leaf out of the otter's book and eat raw fresh-water fish (smoked instead of cooked) they may receive a consignment of broad tapeworms. A knowledge of this one-way food-traffic along food-chains may be of considerable service in narrowing down the field of inquiry when tracing out the missing parts of a parasite's life-history.

It is rather rare for parasites to be important independent links in a food-chain; they are for the most part mere extras on the menu. But there are one or two rather interesting cases where they are eaten for their own sake. The most familiar example is that of the ticks of so many herbivorous mammals, which are eagerly devoured by birds. They may be merely a casual titbit like sheep-ticks in the varied diet of starlings. Or they may be a staple, or even the only, article of diet: the African tick-bird seems to live solely upon the ticks of big game such as rhinoceros, zebra, and antelopes.

One of the oddest cases is that old one, recorded by Herodotus and long dismissed as a traveller's tale, until re-established by the evidence of many nineteenth-century naturalists, of the little plover of the Nile that enters the mouths of crocodiles (held gaping wide to facilitate the bird's task) and picks off the leeches that suck blood from their gums. In the Galapagos Islands a similar rôle is played by a scarlet land-crab, which picks ticks off the big lizards that feed in the surf and come ashore to sun themselves. And there are the white paddie-birds that live in the antarctic and in some places subsist mainly on the round-worms which they pick out in huge numbers from the droppings of nesting penguins. In winter, the penguins move off to the open sea, and the Paddies grow progressively thinner, until the return of the migrants provides a new supply of worms.

§ 7

Storms of Breeding and Death

In the previous section, we pointed out that the abundance of different kinds of animals had a definite relation to their station in life, and their position in a food-chain. In general, the first animal links in such a chain are small in size and abundant in numbers, and each further link is marked by an increase in bulk and a marked reduction in abundance. But we said nothing as to the way in which this regulated equilibrium of numbers was achieved. It will be our business in the present section to give some account of the checks and counter-checks by which the swaying balance is kept within limits and of the consequences, often spectacular and sometimes disastrous, which follow when it is upset.

The first thing to realize is that the idea of a balance, albeit always a swaying balance, is a true one. The numbers of any species depend, on the one hand, upon its rate of reproduction and growth, and on the other upon its death-rate from accident, enemies, and disease, just as the amount of

FIG. 25.—PRIMITIVE MAN OBSERVES A PARASITE CHAIN.

A carving upon basaltic rock from South Africa, reputed to be between 25,000 and 50,000 years old. It represents a white rhinoceros with tick-birds in attendance, even as now.

moisture in the air is a nicely adjusted balance between the number of water-molecules that leave the liquid state every minute in vapour form, and the number that condense again every minute in water.

Were it not for these two opposing forces at work, multiplicative and destructive, life's power of increase would be overwhelming. Before game in Africa was much interfered with by man (indeed, up to less than thirty years ago), settlers in South Africa used periodically to be witnesses of the results of over-multiplication of that little antelope, the springbok. Trekking from the north, the springbok used to pass for days, and several hundred thousand might be in sight at the same moment. One migrating horde was estimated to be fifteen miles wide and a hundred and forty miles long. As a result of the innocent and unrestrained play of their natural instincts they were trekking to misery and death.

In tropical and semi-tropical regions the red single-celled plants called Peridinians occasionally multiply so as to turn the sea to the semblance of blood for miles, and may even be so abundant as to remove most of the available oxygen from the water, thus causing the death of thousands of fish. A few bacteria introduced into the body may in a ten-days' space have multiplied to a population more numerous than all the men and women in the world. A few prickly-pears introduced into Eastern Australia as a botanical curiosity (and for a time propagated and spread by a kindly Society who thought that cactuses in pots might brighten the homes of immigrants' wives) covered thousands of square miles in the course of a few years. At the height of its multiplication the prickly-pear was invading a new acre of Australian land every minute of the day, until, as Dr. Tillyard says: "The vision arose of eastern Australia becoming in about a hundred years' time a vast desert of prickly-pear, with a few walled cities alone holding out against it."

But animals and plants very rarely find a chance of multiplying like this. For most species, the two great checks on increase are enemies and disease. Enemies are generally the

first line, so to speak: epidemic disease rarely steps in unless the species has already multiplied abnormally. It is the out-pacing of enemy checks which accounts for the extraordinary plagues of herbivores in different parts of the world. Let us give an example or so of the pitch that this abnormal increase may reach.

In a mouse plague which occurred in Nevada in 1907, three-quarters of the alfalfa acreage of the State was destroyed. The whole ground, for square mile after square mile, was riddled with mouse-holes till it was like a sieve. It was estimated that the several thousand mouse-eating birds and mammals busily gorging on mice in the affected district were killing over a million mice a month; and yet, in spite of this toll, the numbers of the mice continued to increase. And in the Australian mouse plague in 1917, Hinton, in his booklet on *Rats and Mice as Enemies of Mankind*, records that 70,000 mice were destroyed in one afternoon in one farmyard.

Such a state of affairs cannot continue for long. The multiplying species has escaped from the control of its carnivore enemies; but it must eventually run up against other controls. In the last resort, there is the control exerted by its food: if its multiplication is too excessive, there will not be enough for it to eat. But this control by starvation is a rare event in nature; in most cases, before the increase in numbers has brought the species within sight of food-shortage, a third kind of control steps in—control by disease. Almost all the vast outbursts of rodents end in appalling epidemics which kill off the great majority of the teeming animals and leave the population far below its average abundance. We may quote Soper, a Canadian observer, who is describing the sequel to a great over-multiplication of snow-shoe rabbits: "Empire among the rabbits as elsewhere has its rise and fall, and then is swept away. A strange peril stalks through the woods; the year of death arrives. An odd rabbit drops off here and there, then twos and threes, then whole companies die, until the appalling destruction reduces the woods to desolation. One year (1917) in the

district of Sudbury, Northern Ontario, the signs of rabbits were everywhere, but not a single rabbit could I start. It seemed incredible. Local inquiries disclosed that a little over a year before the rabbit population was beyond count. Now, as if by magic, they were gone. Needless to say, however, a few individuals survive the epidemic. These now, because of their paucity, are seldom encountered."

Another reason why over-multiplication so rarely leads to starvation is that the first pinch of food-pressure is often the signal for great migrations, the animals crowding away from the area of shortage in search of new supplies. Locusts are the classical examples of this behaviour. Their inclusion among the Plagues of Egypt is proof of the impression their appalling visitations made in earlier ages:

> The Lord brought an east wind upon the land all that day, and all that night; and when it was morning, the east wind brought the locusts. And the locusts went up over all the land of Egypt. . . . They covered the face of the whole earth, so that the land was darkened; and they did eat every herb of the land, and all the fruit of the trees, and there remained not any green thing in the trees, or in the herbs of the field, through all the land of Egypt.

To-day their visitations continue unabated in spite of all our civilization. Palestine was recently invaded by crawling hordes of the wingless immature form; in 1925 a plague of locusts threatened Egypt again, but prompt action by entomologists suppressed it; in Algeria and Persia, in South America and South Africa and Russia, serious plagues of them recur every few years. In February 1929 it was announced that Kenya had had to institute a food-rationing system, so formidable had been the inroads of a sudden invasion of winged locusts.

Uvarov has recently discovered a number of interesting facts about the life-cycle of the East European locust. Its main breeding-grounds are in the huge, reedy deltas of the rivers that drain into the Caspian and Aral Seas. Bands of the immature and still pedestrian hoppers leave these swamps nearly every year, sometimes in great numbers.

But it is only periodically, and, it would appear, only after a succession of dry years, that the hordes of adult winged locusts set out. These fly off in all directions; and when their reserves of fat are nearly exhausted, they settle down and fly no more, but lay their eggs wherever they chance to be. If this should be in the middle of crops, immense damage may be done by their offspring. In 1926, for instance, no less than 80,000 acres of wheat, maize and millet were thus utterly devoured in Northern Caucasus alone.

Then comes a strange fact. If the migrating swarm has chanced upon a reed-bed like its own original home in which to lay its eggs, its young develop into locusts of the same type as their parents; but elsewhere most of the young grow up into another type of locust, originally considered a different species. This type is not gregarious, and spreads slowly and individually over the countryside. If it or its young finds a reed-bed, the migratory type is once more produced. Thus from the permanent foci in the big deltas, the species is being disseminated by the armies of hoppers, the periodic winged hordes, and the slow and individualistic spread of the solitary form. And this existence of two forms, one solitary and the other gregarious, has been since shown to hold in several other kinds of locusts.

The ideal method for ridding the world of locusts will be to discover and then destroy their breeding-grounds. Failing this, we must learn to understand and foretell their cycles of abundance and scotch the beasts when they first appear, instead of waiting until their abundance has grown formidable. In any case, their powers of dispersal and the irregular direction of their flights make the locust problem eminently cosmopolitan, one for international control.

Similar outbursts of unbridled reproduction happen with lemmings, the little rat-like creatures that inhabit the moors of the Scandinavian mountains and the lower-lying tundras farther north. Periodically the lemmings, enormously multiplied, invade the lowlands, their huge migrating swarms moving mainly by night. So surprising are these sudden

hordes, appearing as if from nowhere, that Olaus Magnus, writing in the sixteenth century, was convinced that they fell from the clouds. They climb walls and swim rivers, losing many of their number every day. Finally the survivors reach the sea: apparently they take it for another river to be crossed, for they plump in and swim on until they drown. Collett records one case in which a ship steamed for a quarter of an hour through miles of swimming lemmings, and they have been discovered in the stomachs of cod. After such drownings in mass, the winds and currents may heap their bodies in thick drifts on the shore. In any case, of those that leave the mountains, not one returns alive.

In migrating locust swarms there seems to be no disease. But with lemmings, migration and disease go hand in hand. Not all the lemmings leave their homes. Of those that stay behind, the great majority sicken and die, and even of the migrating animals enormous numbers succumb to the epidemic. In some parts of the world squirrels show similar cycles, which terminate in a combination of epidemic and migration. A huge army of migrating grey squirrels swam the Ohio River in 1829; and even bigger hordes are recorded from Russia.

Violent epidemic disease seems to be the natural and inevitable result of overcrowding. Professor Topley, of Manchester, has demonstrated this experimentally in artificial mouse-populations which he has kept at different degrees of crowdedness; and the fact is a matter of common medical and veterinary observation.

This seems to be mainly a mere matter of chance and time. As animals are crowded together, the chances of infection passing from one to another are increased, until, when a certain density of population is reached, the disease, hitherto a smouldering and sporadic thing, becomes a fulminating epidemic—spreading with maximum rapidity throughout the entire population.

Converselv. if the density of its victims falls too low, an

infectious disease may die out. Malaria can only perpetuate itself by travelling to and fro in regular alternation between the digestive tube of mosquitoes and the blood of men.

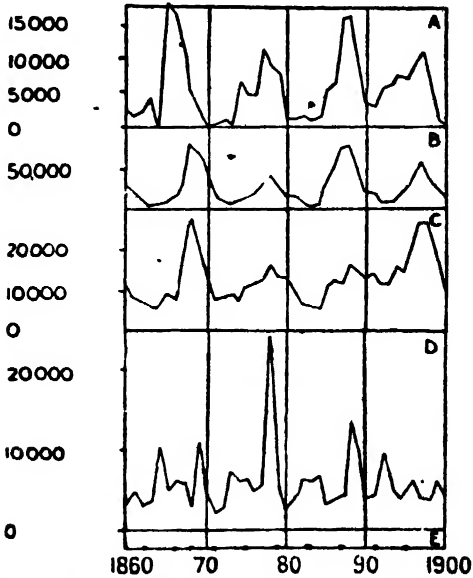

FIG. 26.—THE PERIODIC UPS AND DOWNS OF NORTHERN MAMMALS.

(A), (B), (C), (D) show the number of skins brought in to the Hudson Bay Company from 1860 to 1900. The snow-shoe rabbit (A) has regular peaks about every ten years; the lynx (B) is similar, but the peaks are a year or two later; the red fox (C) shows similar main peaks, with irregularities due to minor oscillations about every three years; the arctic fox (D) shows the three-year oscillations only. (E) Years of lemming migrations in southern Norway. The abundance comes about every four years. (*Modified from "Conservation of the Wild Life of Canada," by G. Hewitt; and "Animal Ecology," by C. Elton.*)

Sir Ronald Ross has demonstrated that if the population either of mosquitoes or of men falls below a certain density in a given area, the proportion of malaria-infected individuals will decrease, slowly but progressively, to nil. In

a not dissimilar way, gun-cotton will burn harmlessly in the air, and remains unchanged altogether when left to itself at ordinary temperatures, when its molecules are relatively calm; but when detonated in a closed space, the violent movement of each molecule reinforces that of every other, and a formidable explosion is the result.

The enhanced rapidity of infection comes not only with artificial crowding, as on overstocked grouse-moors, or in densely packed human cities which have not yet learnt sanitary precautions, but in wild nature too. The abundances of rabbits and muskrats and gerbils and lemmings, even of deer and zebras, the mouse-plagues that the efforts of owls and hawks and men can scarcely palliate, are terminated in a month or so by pestilence; and the few survivors begin the cycle over again.

The next point is naturally to ask what is the cause of the occasional bursts of increase? Here the statistics of trade first put science on to the right track. For over a century, the Hudson Bay Company have kept records of the number of pelts and skins of different kinds of animals brought in to their posts. When these figures are plotted on a curve, they reveal a strange regularity of fluctuation. For almost every species, periods of great scarcity alternate with waves of great abundance; and the peaks of the waves succeed each other in a regular cycle (Fig. 26).

The number of lynx skins brought in every year fell below 5,000 (and sometimes below 1,000) nine times between 1830 and 1914; and in the same period rose above 30,000 (and sometimes above 60,000) the same number of times. The oscillations of snow-shoe rabbits are precisely similar, but even more remarkable, since this species is more subject to disease; in some years epidemics may damp their numbers down to such an extent that only a few dozen skins are brought in. The two curves run parallel with each other, the peaks for the lynx tending to lag behind those for the rabbits. This is what we should expect, since lynxes feed mainly on rabbits.

The increase from the lean years to the crowded years is not a uniform progress, but an acceleration. In the years of great abundance the rabbits will have two or three broods, with eight or ten young in each brood, while in bad years there will be but one brood, with only two or three young to it. The rate of increase itself is thus almost twenty times as great in the favourable years. The numbers of young seem to increase with some regularity, for the Indian trappers are said to prophesy the prospects of next season's rabbit crop by counting the number of embryos in this season's rabbits. The same thing, with a difference, occurs in field-mice. In favourable years, though the number of young in a brood is not increased, the breeding of mice goes on in more months of the year.

A great number of other animals show a greater or lesser degree of regularity in their cycles of abundance and scarcity. Elton in his *Animal Ecology* discusses the whole subject, and makes some interesting general principles emerge. At the opposite pole to the almost clockwork precision of the Canadian lynx and rabbit we have French mice. These indulge in outbursts of over-population, but the outbursts are local and not widespread, irregular instead of regularly recurrent. In such cases the multiplication seems not to be regulated by any cycle of events in the outer world, but to progress irregularly until the population, somewhere or other, reaches the saturation-point for disease. An epidemic then breaks out and kills off the majority of the mice in an over-crowded area, but peters out as it spreads into less populous regions; and the few survivors begin piling up numbers again for a later holocaust.

In lemmings, on the other hand, the variation is not only regular but is synchronous over great tracts of land. Lemmings have a peak of abundance every three or four years, and the years of abundance synchronize almost exactly in countries as thoroughly separate as Norway, Greenland, the North-Canadian mainland and the islands of the arctic archipelago. It is as if they were keeping time to the

beating of some cosmic pendulum. And once the time is set for them, they pass it on to the arctic fox, whose staple food they are. Regularly, every three or four years, the number of arctic fox skins brought in by the Hudson Bay Company trappers falls to 3,000 or under, while in the peak years in between, the number as regularly rises, usually to 10,000 or over.

British mice are rather more regular in their cycles than their French relatives; and they, like lemmings, have cycles of three or four years. The snow-shoe rabbit and the lynx have an even more regular but a longer cycle, with peaks and depressions about every ten years. And the red fox, which is bigger and lives farther south than his arctic cousin, lives partly upon rabbits but partly upon mice. Accordingly, his cycle is a double one, with main peaks corresponding to those of the rabbit, and minor ones super-posed, corresponding to the ups and downs of mice.

Something outside the animals' own lives is imposing this regularity upon them; and that something, it seems certain, has to do with the weather. But what precise factors in the weather thus affect the herbivores is not always easy to say. The readings made by meteorologists, though of the utmost value in abundant ways, are not always very relevant to the life of animals. Temperature, for instance, is usually recorded at a height of four feet in the open and "very few animals live in the open at that height, except cows and zebras and storks and children and certain hovering insects."

Furthermore, what an animal or its food-plant responds to in the way of weather conditions is not likely to be the maximum or the minimum of any one factor, such as temperature or rainfall or sunlight, but especially favourable combinations of several varying factors. To take an example from ourselves: the optimum geographical zone for white men is one of moderate temperature, moderate rainfall, moderate sunshine, and changeable weather; no ex-

tremes are involved in it, and it cannot be defined save as a complex meteorological combination.

The organism integrates the outer forces acting upon it. In the abundances and catastrophes of animals that fluctuate with a regular period we have in reality a new kind of instrument, more subtle than the thermometer or the rain-gauge, which will, we can feel sure, set the meteorologist on the track of new discoveries in his own science.

Sometimes, it is true, the weather does get to work in an obvious way. Very hard winters (which tend to recur with more or less regular periodicity) kill large numbers of the smaller birds. This is apparently due to starvation and not directly to cold. If birds can store up sufficient food, they can withstand astoundingly low temperatures; the little American Junco, even though it usually migrates south in winter and is no bigger than a sparrow, can withstand a blizzard with a temperature of 52° F. below zero, if well fed. The winter of 1928–9 was particularly severe on European bird-life. The hard winter of 1916–17 killed off the longtailed tits so thoroughly over large parts of England that many areas were not restocked up to the normal level of longtailed tit population until two, three, or even four years later.

Many of these animal-cycles seem to have a regular periodicity. The recurrent irruptions of unfamiliar birds are a case in point. The year 1927 witnessed a remarkable invasion of England by that extraordinary bird, the crossbill, which has its mandibles crossed over each other for the purpose of feeding upon pine-cones. These irruptions come westward from the pine-forests of Central Europe, and occur at more or less regular intervals. One in the sixteenth century brought prodigious numbers of the birds, which did great damage by discovering that their beaks were admirably adapted for slicing apples in half as well as for obtaining the seeds from pine-cones. The dates of crossbill irruptions, however, have not been so well recorded as those of two other kinds of birds, the Siberian

nutcracker and the sandgrouse. The nutcracker is an inhabitant of the vast coniferous forests of Siberia. It has invaded Western Europe at intervals of about ten years, with what would be extreme regularity if it were not for the fact that now and again one of the invasions is "skipped." Although observations on the spot in Siberia are not forthcoming, it appears almost certain that the migrations are due to over-population in the birds' natural home, coupled with a bad harvest of the pine-cones upon which they feed. Doubtless, when the failure of the pine-crop is less extreme

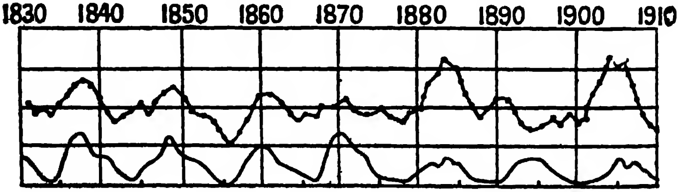

FIG. 27.—THE RELATION BETWEEN SOLAR DISTURBANCES AND TERRESTRIAL LIFE.

The upper curve shows the amount of growth made by trees in Germany, as determined by the thickness of their rings of growth. The lower shows the number of sun-spots recorded by solar observers. There is a considerable agreement between the two curves.

(*Modified from "Earth and Sun," by E. Huntington; after Douglass.*)

than usual, the pressure on population is not so great, and the wave of migration spends itself before reaching Europe.

Pallas' sandgrouse, on the other hand, is a bird of the steppes and deserts of Central Asia, where it lives upon the scanty vegetation of the salty soil. Every so many years the bird leaves its home in huge flocks, migrating both eastwards into China and westwards into Europe, even as far as the British Isles. Sometimes the migrations are continued for two or three years. Here an eleven-year cycle is pretty closely adhered to, with the additional fact that the alternate migrations are larger. However, this may be interfered with by longer weather-cycles, and the irruptions

may not occur when due, as happened in 1930. The cause of the emigration again seems to be relative over-population, or what comes to the same thing, food-shortage, owing to their food-plants being covered by snow or glaze-frost.

A connection has been suspected between the eleven-year cycles and the cycles of sun-spot numbers, which also have an average period of about eleven years. The sun-spots are a sign of increased activity and energy-radiation from the sun's surface; and this causes magnetic storms on our earth, ninety million miles away. Another fact of terrestrial climate which seems to be definitely correlated with sun-spot number concerns the track of thunder-storms. If the tracks followed by heavy storms are plotted on a map, it will be found that, in North America, for instance, there is in any one year a zone along which the majority of storms travel. Now this zone shifts up and down, with considerable regularity, from year to year, returning to the same position about every eleven years. Such a shift in the storm-tracks will obviously mean a slight shift of the margins of all the great climatic zones. It will mean that there will be cycles of rainfall, some areas getting more than the average every eleven years, while other zones in the same years will be getting less than the average; and this, according to the careful investigations of O. T. Walker, is what actually occurs. The autobiography recorded by trees in their annual rings of growth shows that they, in some situations, are under the influence of this eleven-year cycle. Not only does this hold for the giant sequoias of Western America, but a fossil Canadian spruce from the Pleistocene shows that the Canadian climate in those days, certainly over 100,000 years ago, was oscillating with this same eleven-year period.

Such changes are likely to have the most noticeable effect upon plants and animals where conditions are difficult for life. For instance, a small change in rainfall in a semi-desert region will have much more effect than the same change in a well-watered country; and quite small tem-

perature-changes in the arctic will have disproportionately large effects on the animals and plants which live there. Another interesting point that is now emerging is that the most important cycle in warm-temperate regions seems to be the eleven-year one; in regions farther north this gives place to a ten-year cycle, and in the far north, this again to one of about three and a half years. But what may be the explanation of this strange fact we do not yet understand.

The various weather-cycles will have quite different effects on different kinds of animals, according to the length of the animal's own life-cycle. The short-period cycles of three and a half years would only be expected to affect small animals which reach maturity in a year or less. Larger animals have lives which are too long to be upset by such small cycles. In precisely the same way, the choppy little waves which are so unpleasant to the inmates of a rowing-boat have no effect upon the bulk of a liner. Even the eleven-year cycles will have little effect upon animals like deer or zebras. But deer and zebras and others of the larger herbivores do have recurrent plagues in wild nature, and these plagues recur at much longer intervals than those of rabbits; the very length of the cycles makes it more difficult to collect accurate information on them. Some idea of the times involved may be gained from the following rough calculation. If a single pair were to increase with no severe checks, an uncomfortable density of population would be produced by mice or lemmings in about three or four years, by squirrels in about five years, by rabbits or hares in about ten, sheep in twenty, by buffaloes in thirty, and by elephants in fifty or sixty years.

There is one fur-bearing animal which, as the Hudson Bay Company's records show, seems to be exempt from these periodic fluctuations. It is the beaver. The beaver has made itself independent of all the short cycles of weather. It lives almost entirely upon the bark of the trees it fells, which themselves are so long-lived as not to be affected by ten-year or even thirty-year cycles. Then it constructs

remarkable dams and canals which make it independent of all ordinary fluctuations in water-supply. And during the summer it stores great food-piles of trunks and branches in its pond; thus it can get access to food under the ice, and is almost independent of the severity of winter.

When it has cut down too many of the trees in the neighbourhood of one pond, a beaver-community apparently just moves on in search of another; and at the end of summer any surplus population scatters on the same quest. It is on these treks that beavers seem most exposed to the attacks of beasts of prey; and in a state of nature it is then that most of the overplus of the beavers' natural increase is wiped out (just as most of the overplus of migratory birds' increase is wiped out on their migrations). But with their feeding and storage habits, and their normal immunity, safe in their ponds and houses, from most enemies, they have no need of the rapidity of breeding which a mouse or a rabbit must keep up to repair wastage; and so their breeding never runs away with them, so to speak, to lead to sudden huge increases of number. Then, too, their habits compel them to live in isolated colonies; there can never be a dense continuous beaver-population over a large area, and so there can seldom be an explosive outbreak of epidemic beaver-disease. And so the beaver-population (apart from man's inroads upon it) is almost exempt from the wild and rapid fluctuations that beset other rodents. It is regulated within much narrower limits and there is less wastage of lives.

There are other animals in which there is a kind of natural population control. It is found, for instance, among various kinds of birds. Eliot Howard has described and analysed the system in his *Territory in Bird-Life*. In the breeding season, practically all small song-birds have the instinct to stake out a claim, so to speak, to a definite area or territory of considerable extent. This territory they defend against intruders of the same species, and often of allied species as well; they build their nest in it, and they confine themselves

mainly to its boundaries in searching for insects and grubs with which to feed their young (Fig. 28).

This "territorial instinct" doubtless had its origin in the nearly universal impulse to defend the nest and its immediate neighbourhood against intrusion. It takes a great many insects to supply the rapidly-growing naked young of a warbler or a finch; and any extension of the nest-defending instinct to cover a wider area would be of biological advantage to its possessor by reducing the infant mortality of his or her young in times of food-shortage.

When one kind of bird is unusually abundant in any given region, the pressure on space may force down the size of territories. But this process has a limit; a breeding pair will not tolerate another pair within a certain distance of their headquarters, and fighting will go on until one pair or the other are forced to leave. In years of exceptional abundance, some birds never find breeding-territory at all. They may penetrate to the northern limits of the species' range and drift about there in bands; or they may remain celibate in the middle of the breeding population. But they do not breed. So here again an upper limit is set to the population; and we do not find among small birds the same violent cycles, culminating in over-abundance and disease, that we do in small mammals.

When population-pressure seeks relief in migration, opportunity is given for the colonization of new areas. In this way, for instance, every patch of land where locusts could possibly breed is periodically explored by their itinerant swarms; and the same is true for the crossbill. The process is always a wasteful one, and often wholly useless to the animal; none of the myriads of Scandinavian lemmings that leave their mountain home in emigrating armies ever finds a new breeding-ground. And all the Painted Lady butterflies that reach England year by year, sometimes in abundant swarms, are similarly unproductive: they may attempt to breed, but they never establish themselves in this country. Yet these scouts of the species continue

to arrive here in every year of high multiplication. But we must remember that Nature is abominably wasteful; and also that what is useless in one set of circumstances may have some advantage in another. The lemmings of Southern Scandinavia are now confined to a restricted zone of a narrow peninsula. During much of the Ice Age, however, they inhabited the European plains; and then mass-migration might well have brought some survivors into a new and favourable region.

In any case, these periodic ups and downs have a considerable bearing on our ideas about Evolution. In our previous discussion of Natural Selection, we assumed that the struggle for existence exerts a more or less constant pressure. This is not true for species with violent cycles of abundance. When the survivors of a rabbit epidemic, for instance, are restocking the country, the struggle for existence will be very much lightened; as abundance increases, pressure on food-supplies will begin, and will slowly grow. Finally, when the inevitable epidemic breaks out, there is an intense selection at its hands for hardiness and disease-resisting qualities. In the same way, in a very hard winter only the lucky or the resistant birds survive.

In other words, selection itself is a fluctuating thing; and many qualities of plants and animals have been brought into being only by the intense selection of exceptional years. Most of the creatures are not fully tested most of the time; they have a reserve of biological adequacy and could dispense with this or that adaptation during ordinary seasons. But then comes the pinch, and all the reserves are called into play. Periodically the species has, so to speak, to pass special examinations. After a very favourable year, its members are put through a competitive examination first as regards their competency to secure food and breeding-space, and then as regards their disease-resistance; in very unfavourable years they are examined on their power of resisting hunger or thirst and the extremes of temperature. But in between they have a comparatively easy time.

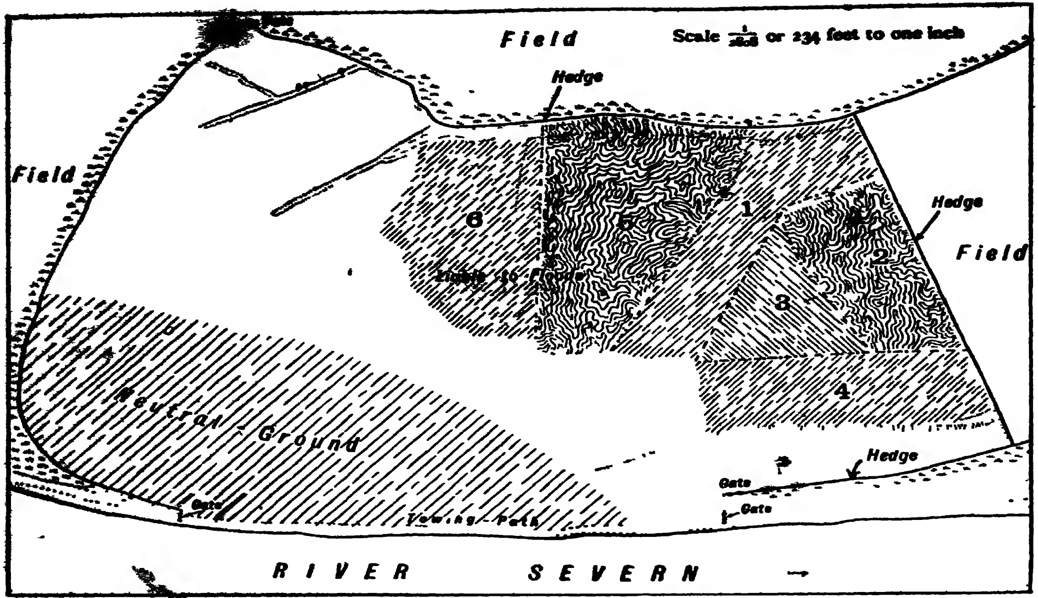

FIG. 28.—THE TERRITORIAL SYSTEM IN BIRDS

Sketch-map of the nesting-territories occupied by six pairs of green plover in 1916 in a meadow in Worcestershire. The field measures about a quarter by an eighth of a mile

(From Territory in Bird Life, by H Eliot Howard John Murray)

The relaxation of selection after a catastrophic killing-off may also have important effects. Characters useless by themselves may be useful if they are combined together; and in these times of comparative ease the species is able to preserve and shuffle its mutations and get the most out of them. A concrete case in point is that of the Greasy Fritillary butterfly. This is a local species, its various stations being widely separated. At one place in the North of England where it had been abundant for a number of years, it suddenly grew scarce. In 1912 it was rare, from 1913 to 1920 very rare. In 1921 it began to increase rapidly again, and has since 1924 remained at its old abundance. During the period of its rapid increase, 1921, 1922 and 1923, it showed a remarkable outburst of variation, in size, colour and pattern. From 1924 on, the range of variation decreased. And now it is as constant as it was before the War—but not quite the same: it is darker, with a coarser-mottled pattern. It looks very much as if, while rapid increase was going on and selection was presumably relaxed, all kinds of re-combinations made by the genes of the few survivors of the previous thinning-out came into being. Then, when population-pressure had brought selection up to the mark once more, most of these were weeded out, and only one main type was left—but it was not the original type. Another combination had been adopted.

But these cycles have more than theoretical interest. There are, for one thing, commercial advantages in knowledge. Fur-trading companies can regulate their staff of trappers according to the prophecies of the ecologist, and can guard themselves against periodic gluts and scarcities of pelts. Much more important is the medical significance of the facts. It is well known that rats act as a reservoir of bubonic plague, transmitting it to human beings by their fleas; and the same is true for other small rodents such as gerbils. It has already been established that in Central Asia and South Africa the incidence of plague in man fluctuates with the abundance of these small mammals. The

year 1910, when a small outbreak of human plague took place in the eastern counties of England, was also a year of plague and apparently of unusual abundance among English rats. In modern conditions, rats are not so ubiquitous as they used to be, nor do they come into such close contact with man; probably this fact saved England from a much more serious visitation of human plague in 1910. The early inhabitants of Palestine seem to have had some inkling of the connection between rodents and disease. In 1 Samuel, chapters v and vi, we are told that the Philistines, afflicted with a grievous pestilence which seems to have been bubonic plague, were recommended to make and offer up golden images not only of the swellings or buboes, characteristic of the disease, but also "of the mice that mar the land." Modern biology has verified this connection in detail, and shown the real nature of the relation between the fluctuations of the species rat and the danger of human infection.

A recent application of this knowledge probably saved South Africa from a serious visitation. The gerbil is a common rodent of this and other warm-temperate regions. In 1924–5 the gerbils over a large extent of the Union were plague-infected, and the area of gerbil-infection was still increasing rapidly. In a belt of country south of the infected area a war of extermination was waged against gerbils and all other plague-carrying rodents, and the epidemic passed away before reaching Cape Town and the populous coast, owing to the natural dying down of the disease-stricken gerbil population to a density at which plague would no longer spread through it.

And it may well be that other epidemic diseases whose comings and goings are still mysterious will prove to be linked with the abundance or scarcity of some obscure rodent; but here only laborious research can enlighten us.

These facts help us to realize the real nature of the ordinary Struggle for Life. The careless thinker about things biological is apt to fall under the sway of military ideas and think of it as a war between one species and another. He

envisages it as a regular battle between an inoffensive herbivore and its enemies, or a sort of athletic competition between a carnivore and its prey. In both cases he thinks of the struggle as something in which victory is to be achieved as it is achieved in war or sport. As a matter of fact, it is nothing of the kind. A herbivorous species without carnivorous enemies would tend to overpopulate its territory, would become diseased and under-nourished, would condemn itself to starvation by eating down its own food-supply; a carnivorous species again which was restricted to one kind of prey, and a kind it could too easily catch, would inevitably bring its own race to extinction by eating itself out of existence. To multiply and replenish the earth unchecked may be only the prelude to decay and extinction. Both of these eventualities have, through the interference of man, been realized. When red deer were introduced into New Zealand, they throve on the succulent forest and bush and multiplied exceedingly owing to the absence of all carnivorous enemies. But after a few decades they had changed the face of the country where they were abundant, and to-day the fine heads and heavy beasts are found only on the outskirts of the deer's range, where they are still advancing into virgin country. Elsewhere the herds, living on scarce and inferior food, are full of stunted specimens with malformed antlers, and the authorities have been forced to play the part of natural enemy, and to adopt a rigorous policy of periodic thinning-out to save the stock.

For a carnivorous instance of the evil of easy living we may quote from Elton the curious case of Berlenga Island, off the coast of Portugal:

> This place supports a lighthouse and a lighthouse-keeper, who was in the habit of growing vegetables on the island, but was plagued by rabbits which had been introduced at some time or other. He also had the idea of introducing cats to cope with the situation—which they did so effectively that they ultimately ate up every single rabbit on the island. Having succeeded in this, the cats starved to death, since there were no other edible animals on the island.

We are often told that it is very important for children to select their parents wisely. It is becoming clear that a wise choice of enemies is an asset to an organism ! One can hardly, perhaps, speak of an animal's enemies as part of its adaptations, but at least they are vital to its survival. In almost every case the word *enemy* is only applicable when we are thinking in terms of individuals : as soon as we think of species, the individual " enemy " often turns out to be a racial benefactor.

CHAPTER VI

LIFE UNDER CONTROL

§ 1. The Balance of Nature.
§ 2. Pests and their Biological Control.
§ 3. The Beginnings of Applied Biology.
§ 4. The Ecological Outlook

§ 1

The Balance of Nature

THE fluctuations in animal numbers we have been discussing give us new insight into the tangled web of interrelations summed up in the phrase "The Balance of Nature." A few further instances of the swaying of that balance may be interesting and profitable.

Change in one member of a life-community may transform the whole community into something else, as surprisingly as an increase of thyroid secretion will transform an axolotl into a land salamander. A classical case is that described by Ritchie in his interesting book, *The Influence of Man on Animal Life in Scotland.* It concerns a small stretch of moor in Southern Scotland. When the story begins, this was covered with heather, and tenanted by typical heather-moor creatures such as the red grouse. In 1892, a few pairs of black-headed gulls came to nest there. This was probably the result of a general increase in the numbers of their species, but what produced this increase we do not know. Whatever the reason, the fact was the starting-point for an intricate chain of cause and effect. The owner liked the gulls and protected them, with the result that by 1905 there was a

nesting colony of over 3,000. The trampling of the birds was bad for the heather, while their constant manuring of the ground changed the character of the soil. The result was that the heather vanished altogether, its place being taken first by rushes and later by coarse dock-like plants. Pools of shallow water formed here and there. With the heather, the grouse disappeared, while the pools attracted teal and other duck. In 1905, protection was withdrawn from the gulls, their nests were robbed, and they decreased rapidly, until by 1917 there were only a hundred or so of them left. The heather had re-invaded most of the ground, the pools were drying up, the teal had gone, and the grouse were returning. Thus in twenty-five years the ground and all its plant and animal inhabitants had changed completely, and then changed back again.

Another well-analysed case comes from the Brecklands of East Anglia. The natural dominant vegetation of this strange barren country seems to be low pine-wood. Wherever the trees for one reason or another fail to grow, dry heather-moor takes its place. Patches of thick-growing bracken-fern and low-grass heath also exist. The most abundant of the vertebrate inhabitants is the rabbit.

Rabbits are not indigenous to England. After the Ice Age they failed to reach it before the Channel had put a bar between it and the rest of Europe. They were certainly not introduced before the Neolithic Period, and many authorities believe that they were not brought over until after the Norman Conquest. However introduced, during the Middle Ages they were protected in warrens for the sake of their skins, but eventually spread and multiplied as they have in other countries. Their attacks on the pine-seedlings, together with the clearing and felling due to man, have swept the natural pinewood off the plateaux, and left heather to take its place. A natural equilibrium was soon established between rabbits and their enemies such as stoats and weasels, and lasted for centuries. Of recent years, however, civilization in general and game-preserving in particular have

enormously reduced the number of these carnivores, and the rabbits, relieved of this drain on their numbers, are increasing towards a new equilibrium of much greater abundance. The resultant " rabbit-pressure " is in its turn having striking effect upon the vegetation. Wherever the rabbits have access to pinewood, it fails to reproduce itself, and its place is taken by heather. But the heather, which could stand a certain density of rabbit-numbers, itself melts away when their concentration rises above a certain point. It is eaten down, and gives place either to rush or to grass-heath. If rabbits are not too abundant, the outcome is decided by the nature of the soil; but once more the animals have the casting vote. If the pressure for subsistence is great, they attack the rushes, and these too are replaced by grass-heath.

The grass-heath itself is badly attacked by the rabbits; it is stunted and nibbled down close; and yet it can survive where the rushes and heather die out. As Farrow says: " The grass-heath owes its very existence to an extremely injurious influence which nevertheless greatly benefits it because it injures its competitors slightly more." Increasing rabbit-pressure, it will be noticed, progressively reduces the height of the vegetation. Pine-trees yield to bushy heather; heather to scrubby rushes; and rushes to the mere carpet of the grass. In normal circumstances the advantage given by height in the struggle for light and air causes a succession from low to tall plants, culminating in forest; and this is what happens in Breckland wherever rabbits are fenced out. But with intense rabbit-pressure, the contrary is the case, and the plant which can live and reproduce though cropped down to a mere inch or so will survive.

A complication is introduced by the bracken; for this, though tall and juicy, is distasteful to rabbits, and they leave it alone unless very hard put to it. As a consequence a miniature jungle of bracken is spreading rapidly over the landscape. Should it come to cover most of the country, the rabbits would be confronted by a new problem; they would have to eat bracken or starve. They would eat it;

and so a new tilt would be given to the ever-unstable balance.

Thus the destruction of weasels and stoats has set the different kinds of plants advancing and retreating, marching and counter-marching, over all Breckland, and it is only because they march by yards in a year, instead of miles in a day, that their movements do not strike us as immediately and forcibly as the manœuvres of troops or the migration of birds or lemmings.

Both these cases provide good examples of a general principle—that change in life-communities goes by jumps, even though the change in conditions alters slowly and gradually. A change in the number of rabbits does not merely alter the proportion of pine-trees and heather-bushes and rushes and grass plants, but causes the total replacement of one kind of plant by another over a stretch of country. This is simply a particular aspect of the familiar fact of dominance, which we meet with in every plant-community.

Of the subtlety of the web's weaving, whereby a twitch on one life-thread alters the whole fabric, many writers have told us. A very simple case is the connection of ravens with sheep-farming. In early spring the staple diet of ravens on the Scottish hills is afforded by the afterbirths of the ewes that have lambed. If sheep-farming ceased to be practised in Scotland, the number of ravens would go down with a bump.

A more curious example is the Box and Cox habits of mongooses and gerbils. The gerbil, a social creature, is a little burrowing rodent of the South African veldt; the yellow mongoose is a stoat-like carnivore inhabiting the same regions. Both retreat underground for safety; and it frequently happens that they live side by side, or even share some burrows and runways in common. Usually, however, their two streams of life do not come into more intimate contact, for the mongooses come out to feed by day and only use the burrows to sleep in at night, while the gerbils sleep through the daylight and are purely nocturnal feeders.

However, when the gerbils are smitten, as is the fate of small rodents, with epidemics, they often crawl miserably out of their burrows by day, and then are caught and eaten by mongooses. One of the most frequent diseases of gerbils is bubonic plague. The ecologist accordingly examines the excreta of the mongoose; when he finds gerbil fur in them, he knows the gerbils are dying of some epidemic, and that this is more likely than not to be plague; and so he can either pursue his investigations further to make sure, or he can at once, though with a chance of being mistaken, recommend human precautions.

Many people have heard of Darwin's celebrated example of cats and clover. He pointed out that red clover, an important forage-crop, was absolutely dependent for its fertilization upon the visits of humble-bees, hive-bees not having a long enough proboscis to reach the nectar. Humble bees make underground nests in banks and slopes; and these nests are often raided and destroyed by field mice, one observer estimating that this fate befalls over two-thirds of all the humble-bees' nests in England. The number of field-mice, especially near villages, is partly controlled by cats. And in this way, said Darwin, a decline in the number of cats would bring about a reduction in the amount of seed set by red clover.

Modern ecology is inclined to criticize this statement so far as cats are concerned. It would need a vast multitude of cats to affect the mouse population very seriously. On the other hand, there is undoubtedly a close connection between the mice and the bees; so that the ups and downs of the mouse population will certainly affect the crop of clover-seed.

Miss Turner, the well-known student of bird-life, has pointed out the connection between the growth of motor traffic and the decline of certain species of bird. Sometimes, as we all know, this connection is obvious enough. The sparrow has almost vanished from the central parts of many American towns now that he is deprived of horse-droppings and scattered grain from nose-bags. But here is a subtler

chain. In those remote days (a quarter of a century ago) when horse-buses were the Londoner's main means of transport, much of the horses' fodder was supplied from Norfolk. The rank marsh-grasses were regularly cut, ground into chaff, and sent off to the omnibus companies in London. The marshes that were cut in any one year provided ideal nesting-grounds for small waders and plovers the next season. To-day there is no market for marsh-grass. It grows dense and tall, and often is replaced in natural process of ecological succession by thick sedge. The snipe and redshank and plover can no longer force their way through this coarse tangle; and so fewer of them can breed in Norfolk and their races decline there.

Sometimes these obscure linkages have important practical results. As we have pointed out, the blackberry, imported into New Zealand, has there changed from a harmless weed, which compensates for its thorns by its contribution to jam, to a real pest. But it is doubtful if it would ever have done so but for the introduction of European birds into the country. Some of these, notably the starling, devour its fruits, pass the seeds out undigested, and thus multiply its power of dispersal. Without this aid the invasion of new territory would probably have been so slow that the plant could easily have been kept in check.

§ 2

Pests and their Biological Control

All over the world man has been busy making difficulties for himself. The crowding of human beings into cities, like the crowding of animals in their times of over-multiplication, give new openings to disease. The city is the fosterer of commerce and architecture, of learning and the arts; but until it is disciplined and controlled, it is also the opportunity of the bacterium. Freedom of intercourse and communication stimulates both trade and thought; but it gives

disease-germs new facilities for rapid spreading, as when the opening up of Africa brought sleeping sickness across from the West Coast to the East. Thus the growth of civilization has been marked by a trail of plagues, more explosive and more widespread than anything which primitive man can have experienced.

Agriculture brings similar difficulties. City life crowds and agglomerates human beings. Agriculture crowds and agglomerates single kinds of plants and animals; and the more thoroughly and intensively it is practised, the denser the agglomerations and the more unnatural the massing. This crowding not only gives new opportunities to the fungi and bacteria and protozoa that are the causes of most animal and plant diseases, but is an open invitation to insects. This is notably so in the tropics, where insects are more abundant and their life runs quicker. Tropical agriculture, though it gives promise of huge additions to the world's supplies of food, is not merely an invitation but an incitement to insects. And the greater the excellence of communications, the more chance of introducing lurking and often unsuspected pests from one part of the world to another—rats and earwigs, forest-devouring caterpillars and crop-choking weeds.

Again, the bringing in of the products of one region of the globe to supply the natural deficiencies of another is an obvious way in which man may improve upon nature. One has only to think of the food and recreation now abundantly provided in many previously barren mountain streams of the Rockies and the Bighorns by the introduction of trout, or the beautification of Europe or American gardens by the flowers of China and South Africa. But here almost more than anywhere else it behoves the would-be benefactor of humanity to proceed with caution; if he is not careful he will do infinitely more harm than good.

Of late years, considerable progress has been made with a difficult art—the biological control of pests. The art itself is very old—at least as old as the habit of keeping cats to kill mice—but recently it has been greatly refined and

elaborated. Almost invariably, a pest is an animal or a plant which has been introduced, whether deliberately or accidentally into a new country. Among the few exceptions, one is so interesting that we must cite it. The kea of New Zealand is a large and more or less omnivorous mountain parrot. Some time after the introduction of sheep into New Zealand, it was found that the kea in certain regions had taken to sheep killing. They settled on the sheep's backs and tore away with their powerful beaks until they exposed the wretched animals' kidneys, which they devoured, killing the sheep in the process. Presumably they must have originally mistaken the sheep for moss and lichen-covered rocks, and in scratching for insects, have found warm meat. In this case it was the introduction of new food which turned a harmless creature into a pest. A similar though less striking example comes from Africa. The birds known as ox-peckers were adapted to picking parasites from the tough hides of rhinoceroses. When domestic cattle were introduced, the birds turned their attention to them too. But here they often penetrated the skin. When the flesh is thus exposed, they seem not averse to it, so that they too are on the way to become a nuisance.

When new species are introduced into a country, few will find themselves in the same balance as in their old home. For the majority, things will be unfavourable; they fail to gain a footing, and some disappear. Now and again, however, the introduced species chances to be better suited; and then its numbers will go up, often far beyond anything possible to it in its native country; and not infrequently its abundance will force it into changed habits. The starling in America has spread steadily since its introduction, and is reducing the numbers of many hole-breeding American birds by occupying so many of the limited supply of nesting sites. And once its population-density oversteps certain limits it is forced to change its food habits, and does a good deal of damage. In moderate numbers, starlings (and the same is true for a number of other creatures) do good, on balance;

in great numbers they do harm. The earwig, a mere nuisance at home in Europe, has become a voracious and serious pest in New Zealand and the Pacific Coast of America, where some States have even set up special Bureaux of Earwig Control. The thistle was introduced into California by a Scotsman who wished to have his native emblem growing on his land; but it multiplied and infested the lands of everyone else. Another patriotic Scot in New Zealand built a fence round the first thistle that appeared on his farm, to protect it from possible enemies; but it was the advance-guard of a formidable invasion. Thompson's interesting book, *The Acclimatization of Plants and Animals in New Zealand*, is full of similar examples of misguided zeal. English sparrows, for example, were introduced so that their matutinal chirpings might help the early colonists to forget their home-sickness.

The musk-rat, a water-rat measuring about a foot from tip of nose to root of tail, is a native of North America. In 1905, three females and two males were introduced to an estate near Prague so that they could be farmed for their fur. Some of their descendants escaped and the resulting musk-rat population expanded with almost explosive violence. In 1927 it was estimated that about a hundred million musk-rats were established in Central Europe, all descendants of the original five. They do untold damage by undermining the banks of rivers and canals. With the same object in view the animals have been introduced into England, where in many districts they have become a serious pest.

Not infrequently, notably with insects, the devastating increase of an introduced species is due to its having arrived without its proper parasite enemies. If the right parasites can be found and turned out in quantity, the missing control is resumed, and in a very short time the pest is reduced to harmlessness, or at least manageability. A good case is that of the Gipsy Moth, *Lymantria dispar*. This is a terrible enemy to trees, and even in its native Europe it will from time to time enter upon a period of over-multiplication and do

enormous damage to forests. But in America, where it was introduced in the late nineteenth century, it threatened to develop into a new Plague of Egypt. Over wide stretches of country it stripped every tree of its leaves, and when the trees were finished, the hungry armies of caterpillars came down to earth and took to eating the herbs and flowers. An extraordinary sound fills the forest when the caterpillars are at the height of their abundance. Even on the stillest day there is a continual rustling patter; it is the sound made by their innumerable droppings.

It was found that the moth had succeeded in entering the country without any of its insect parasites; when three of the commonest of these were imported they imposed a new equilibrium on the population of the species, and it became no more of a pest in America than in Europe.

One of the most striking examples of biological control comes from the Fiji Islands. Here, as on so many of the islands of Oceania, the coconut palm is one of the most important of vegetables, yielding not only many products for local use, but also the valuable coir fibre and the still more valuable copra, in which there is an extensive trade. Towards the end of the last century, the coconut plantations of Viti Levu, one of the two large islands of the Fiji group, began to fail. All sorts of soil investigations were made, but it was not for some years that anyone thought of looking for an insect enemy. It disclosed itself as soon as looked for —a lovely little purple-winged moth whose caterpillars devoured the leaves. The pest grew worse and worse, until in some plantations the trees were reduced to bare poles. So far the pest had been confined to the one island; then suddenly in 1922 it appeared on two small islands on the way between Viti Levu and Vanua Levu, the other big piece of land in Fiji, whose annual coconut crop was worth half a million sterling; and in 1923 took a further step to a new island. The planters now began to feel desperate. They offered a prize of £5,000 for a cure for the pest; but on its being pointed out to them that such a discovery would

inevitably be the result of many men's brains, wisely changed their plan for one of deliberate research.

It had been discovered that the coconut moth in Fiji was exempt from parasites. Three entomologists were set the task of finding a parasite for it. They searched the coasts of the Pacific; and one of them in Malaya found a related moth which was parasitized by various enemies, the most important being a certain kind of fly. The next step was to get the parasites to Fiji. This was not so easy, as they do not hibernate. However, by chartering a steamer to make a special voyage direct from Malaya to Fiji, 300 flies were brought over in 1925. By twelve months later over 32,000 flies had been bred and set free, and by 1928 the fly had not only established itself wherever the moth was to be found, but was attacking between seventy-five and ninety per cent. of the caterpillars. From Java two more parasites were introduced later, a second fly to prey on the caterpillar stage and a tiny wasp-like insect which is a parasite of the eggs. The result, three years after the first parasites were liberated, was that the moth had become quite rare, and that at a total cost of a few thousand pounds an important industry had been made safe, from one fatal enemy at least, in perpetuity.

In Puerto Rico, the sugar-crops were being ruined by beetle grubs. But the situation was saved by the importation of giant toads from Barbados and Jamaica. Here we have an instance of the introduction, not of a parasite but of a predator.

This kind of work has its difficulties as well as its triumphs. The sugar-cane borer is a little weevil that was doing a vast deal of damage in Hawaii in the early years of this century. Muir set out to find a parasite, and eventually, after over two years of hunting round the Pacific, discovered one in Amboina, off the coast of New Guinea. But Amboina is 4,000 miles from Hawaii; and the fly has a short life-cycle, and is very difficult to breed in cages. Eventually, after a number of failures (for instance, Muir developed typhoid at

sea, when travelling with his flies, lost them all, and was forced to go back to Amboina and begin all over again), the fly was brought to Hawaii by stages—first to Queensland, where a new generation was bred, then to Fiji for a second generation, and so to Hawaii. Once it was introduced in Hawaii it soon reduced the sugar-cane weevil from serious pest to minor nuisance.

Biological control of plant pests is also possible, though both more difficult and more risky. You have to find an insect which will eat your weed and preferably nothing else; at any rate it must not eat anything of use or value. By the aid of this ally you may arrest the spread of your pest, and then can proceed to measures of destruction—up-rooting and the like—which are of no account whatever when the plant is in the full tide of its unnatural increase.

Considerable progress has been made by this means towards checking the onward march of the prickly-pear in Australia. It was at one time suggested that the spines should be burnt off and the plants used for feeding cattle; but it was pointed out that the annual increase of prickly-pear was considerably greater than the eating capacity of all the stock in Australia! It was eventually decided that the only hope lay in biological control. A well-financed scheme of research was brought into being in 1920. Entomologists scoured the United States, South America and the West Indies for enemies of prickly-pear and related kinds of cactus. For these a breeding-station belonging to the Australian Commonwealth was set up in Texas, and special methods of transport were devised. Among the dozens of insects tried out, four main kinds have been liberated on a large scale—caterpillars of the moth Cactoblastis that tunnel through the plant; plant-bugs and cochineal insects which suck its juices, and the "red spider" (really a mite) which nibbles its surface. These are all confined to prickly-pear, and actually starve to death on any other plant, so narrowly specialized are their feeding-habits.

With the aid of these auxiliaries, the progress of this

unpleasant vegetable has now apparently been checked. Australian land is no longer being covered with impenetrable prickly scrub to the extent of a thousand square miles (an area over the size of Warwickshire) every year; and Australian civilization has a breathing space to look round for other insect weapons to complete the pests' destruction.

To help in this work of biological control, special laboratories have been established in many countries. Perhaps the most remarkable is one near London attached to the Imperial Bureau of Entomology. In this "Parasite Zoo," biologists work out the methods of rearing all manner of insect parasites, and ship them in bulk to all parts of the British Empire as they are required.

But biological control is not always practicable. It is rarely possible, for instance, for man to employ vertebrates as his auxiliaries in this way, for the simple reason that they, with their more plastic nervous systems, will not consent to remain tied to one kind of food after the manner of so many insects. They have the habit of switching over even from their favourite diet, should it grow scarce, and taking to another which happens to be more abundant.

This habit has obvious dangers where a mammal, for instance, is introduced to cope with a pest. The most celebrated case of this kind is perhaps that of the mongooses introduced into the West Indies to cope with a plague of rats. They reduced the rats to a certain extent, but as the rats grew scarce, turned their attention to other creatures, especially wild birds and poultry; and speedily became a pest almost as bad as the one they had removed.

For pests with a complicated life-history, increase of knowledge may sometimes reveal unexpected methods of control. There is, for example, a disease of the white pine, known as blister-rust, which may inflict great economic loss. This, like other rust diseases, is caused by a fungus which requires two hosts to complete its cycle of reproduction. The white pine is the first; the second is wild gooseberry. If we can extirpate wild gooseberries, we can get rid of blister-rust as

surely as we can stop men and women having malaria by extirpating certain kinds of mosquito. This can be undertaken by direct methods. But a study of ecological succession has shown how good forestry will help on the extirpation. Where a clearing in the forest (the matter has been studied in New England and the Adirondacks) is left to itself, the first stage of weeds and shrubs gives place after a year or so to shrubs and bushes, among which the wild gooseberries find a place. And these are succeeded by a forest stage, with white pine, maple, and other trees. Now the seeds of the gooseberry are dispersed in the droppings of fruit-eating birds; and it so happens that when the forest stage is reached, these gooseberry-eaters no longer find the place to their liking, and depart for other clearings. The gooseberry plants still manage to survive under the shade of the trees, but in the absence of their natural disseminators they do not spread and multiply. It is only in open shrubby clearings that they can increase. The proper reforestation of cut-over parts of the forest, with a little judicious weeding among the young trees, will help reduce the gooseberry bushes, and so the rust.

§ 3

The Beginnings of Applied Biology

In these and many other ways, man is beginning to turn his all too scanty knowledge of the ecological web to good account. Apart from economic difficulties, most of the problems which agriculture has to face, and many of those which beset medicine, are problems in applied ecology. This is especially so in new countries and tropical climates. Knowledge is already so diversified that we partition up the task among a panel of specialists—soil chemists, entomologists, experts in moulds and fungi, agronomists, foresters, bacteriologists, public-health experts. But the problems interlock and shift from one field to another. The ento-

mologist, faced by a disease of crops, will make it his business to look for insects; he may find them all right—and yet their undue abundance may be only the symptom of a weakened resistance of the plant, due to an attack of fungus, or to wrong methods of cultivation. The control of sleeping sickness, malaria, and yellow fever, we now know, depends upon a knowledge of the numerous species of tsetse-flies and mosquitoes and a full understanding of their habits. Medicine here would be helpless without the museum systematist with his vast collections, and the field entomologist, busy observing the insects' ways.

But even ecology, wide though it be, is not wide enough. Physiology and genetics, embryology and bio-chemistry and other sister sciences must also join in the counsels of applied biology if she is to rise to the level of her opportunities.

As J. B. S. Haldane has pointed out in his *Daedalus*, biological inventions have up to the present been few, and most of them were made before the dawn of history. Of these early achievements there is the domestication of animals, and the domestication of plants that we call agriculture. There is the utilization (doubtless not made without the overcoming of much sacred repugnance) of the milk of other creatures; there is the harnessing of yeasts and bacteria to make alcoholic drinks and vinegar and curds and cheeses. Perhaps, as he suggests, legends like that of the Minotaur hint at widespread and startling essays in hybridization; whatever the truth of this, certainly the discovery that stocks of animals and plants could be improved by crossing and selection, however unconscious the methods may have been at the start, is to be reckoned as another great biological invention. So was the idea of the rotation of crops; so was the practice of grafting; so was irrigation; so was the employment of castration to render domestic animals tamer and fatter, and so, too, was the deliberate practice of surgery. All these date back to prehistoric times; and from then until quite lately the tide of biological invention stagnated; any

progress lay almost wholly in the improvement of what already existed.

The eighteenth and nineteenth centuries saw the tide begin to flow again. There was the discovery of artificial insemination by the Abbé Spallanzani; the use of chloroform as an anæsthetic by Sir James Simpson; the invention of artificial manures by Liebig; Pasteur's discoveries about immunity, which made it possible for some diseases previously thought intractable, like rabies, to be cured, and others, like typhoid, to be deliberately prevented; the utilization by Lister of Pasteur's discovery that putrefaction was caused by living bacteria, to give the world antiseptic and then aseptic surgery; the invention of new methods of controlling diseases, such as yellow fever and malaria, made possible by the discoveries of Manson, Ross, and Grassi as to the rôle played by insects in their transmission; the discovery of how to isolate and bottle up the active principles of the organs of chemical control, such as thyroid and adrenal, for use whenever needed —these are some. Another biological invention of this period must be mentioned, and that is the invention of safe and simple methods of preventing conception; for whether we approve or disapprove of their use we cannot but admit that their invention opens the door to momentous consequences.

Matters are moving a little more quickly in this twentieth century. Neither Loeb's great discovery of how to make unfertilized eggs develop, nor the equally remarkable discovery of tissue-culture, has as yet received any practical application. But we have made a beginning with this business of biological control of pests; we have begun to supplement the empirical practices (often admirable in their way) of the plant- and animal-breeder with the application of Mendelian principles; and in a few places we have made a timid beginning in applying our knowledge of heredity to the improvement of our own species. We are making steady progress in the task of finding a drug which will produce healthy sleep without evil after-effects. The dis-

coveries concerning vitamins and mineral salts and food-balance are making possible the invention of a healthy diet for city-dwellers; those concerning the effects of ultra-violet rays and radiant heat are on the way to give us healthy houses, and in time, let us hope, fogless towns. And we have had the invention of a method, however imperfect as yet, for rejuvenation.

The list, it will be perceived, is not a long one; and it is out of all proportion to the biological imaginations of mankind. Man has dreamt of prolonging his life; of controlling the destinies of society as he can now control a business or a machine; of eliminating pain; of building a new race, all of whom should be strong and beautiful, clever and brave and good; of harnessing the forces of life to work for him as effectively as he has harnessed the forces of lifeless matter; of creating living matter anew; of getting rid of disease; of making synthetic food and drink and substances which should stimulate and enlarge this or that faculty without being followed by depression or injurious effects; of fashioning new kinds of animals and plants as easily as he fashions clay or wood or metal; of painless, quiet and happy dying; of the abolition of fear and worry, cruelty and injustice; of an intensification of human capacity for living—the abolishing of fatigue, the enhancement of vigour and enjoyment; of making life yield happiness, or if not happiness, then joy and divine discontent.

Those are dreams that depend for their realization on the sciences of life; and what a paltry beginning we have as yet made with their realization! This is in part due to our refusal to use the knowledge already available to us; but to a far greater extent it is due to a lack of knowledge. Without a thorough knowledge of the abstruse and apparently academic principles of physics and chemistry not a single motor-car or wireless set, let alone an aeroplane or a television apparatus, could ever have been built; and we must get to know much more about the chemistry and physics of living matter, its psychology, the laws of its heredity, the mode of

development of its body and its mind, before we shall be able to satisfy man's biological ambitions.

We may give one or two examples of the way in which the problems of applied biology are opening out. Let us take first the problem of the world's grass. The story begins with the veterinary surgeons. They told of diseases which mysteriously affected cattle, pigs, sheep and horses, their growth and condition, their fertility, and their yield of meat, milk or wool. Eventually these diseases were traced to a deficiency of diet; the animals were not getting enough mineral salts in their food. Sometimes it was iron that was deficient, sometimes iodine; not infrequently calcium, and most often phosphorus. Vast tracts of land in Africa, in Australia, in the west of Scotland, in the United States, are short of one or other of these vital elements.

Wild animals could thrive and reproduce in these regions because in nature a balance is automatically struck; the country carries what it can carry. Moreover, when the animals die, the materials of their bodies return to the soil.

When man comes on the scene, matters are altered. He crowds the country with animals. He hurries up their growth and increases the demands they make on the soil. A modern cow gives about a thousand gallons of milk at one lactation period, and produces her first calf at about three years; the native cattle of Africa do not breed till they are six, and yield at most 300 gallons of milk at one lactation. And too often he ships off the meat, bone-meal, cheese, leather, and wool without putting anything back in the soil. He forgets that all their mineral ingredients have come out of the soil. A country that is exporting grassland products is also exporting grassland fertility. There are large areas which are naturally deficient in minerals; but man has been creating mineral deficiency over other and vaster areas.

In untamed country, animals, wild and domestic, may make up for mineral defects by making periodic journeys to salt-licks and storing their systems with the elements

they need. But when the lands grow settled, fencing interferes with these pilgrimages, as it has, for instance, in Kenya.

Once the diseases of cattle had drawn attention to this problem, research pursued clues in new directions. It was found that the amount of calcium or other mineral elements in the soil which was enough to prevent disease was not nearly enough to allow animals to give their maximum yield. Most pastures can have their stock-carrying capacity materially increased by adding mineral fertilizers. Then it was discovered that different grasses were by no means equal in their demands and their performance. In some dry countries, if you provide the right brand of salts and the right breed of grasses and clover, you can without irrigation turn a mean, scrubby pasture into a rich sward. You can breed grasses which will grow twice as fast as ordinary wild grasses. You can import new breeds of grass as you now introduce new strains of maize or wheat. In New Zealand, for instance, there are no indigenous animals that graze; and when cows and sheep are introduced the native grasses fade out under the unaccustomed nibbling. The New Zealand pastures can only continue productive if the right sward-plants are imported. Science is now making a resolute attack on the problem. Co-ordinated work like that of the Grass Research Station at Aberystwyth is making a good beginning; from these Welsh uplands new varieties are destined to be sent all over the world.

We have already bred animals that can build meat and milk and produce new meat-and-milk machines like themselves twice as fast as the wild representatives of their species; if we take half the trouble with the genetics of grass and clover which we have already taken with wheat and corn, we can make pasture that grows twice as fast as the average pasture of to-day; and if we pay attention to the elementary chemistry of the soil, we can ensure that this doubled demand shall be satisfied. The value of products which come out of grassland is enormous—as much as that of all

our cereal crops together. If we like, we can double or treble this enormous yield.

From grass we may pass to wheat. The wheatfields of the world (we are citing Sir Frederick Keeble's *Life of Plants*) cover about 400,000 square miles, and the average yield is about thirteen bushels to the acre. A bushel of wheat weighs some sixty-three pounds, so that this amounts to just about 100 million tons. There are 1,625 calories of energy-value in a pound of wheat, and the average number of calories needed to keep a man going for a day is about 3,000. So, if we translate our wheat into terms of energy, and "if man could and did live by bread alone, the wheat crop of the world would each year provide sustenance for wellnigh 300 million men."

No wonder that the world's wheat-belts are important. They can be made more important in various ways—by improved agricultural practice, by breeding disease-resistant strains, and so forth. Here we will only consider one way. They can become more important by being made to grow larger—through the breeding of special strains which will creep up towards the pole by growing and ripening earlier. Every day taken off the average time needed for a wheat to ripen means so many more miles advance of the wheat-belt northward.

In the early years of the present century the three Saunders, father and two sons, bred a new wheat called Marquis. It ripened a week to ten days earlier than Red Fife, which had been for years the staple Canadian strain. Between 1911 and 1916, Marquis superseded Red Fife, and the limit of wheat-farming was pushed fifty miles to the northwards. Since then other wheats have been invented which live at an even quicker rate—Ruby, Garnett and Reward; and wheat has been brought another forty miles nearer the north pole. There must be a limit to the process; but it has not yet been reached.

§ 4

The Ecological Outlook

Let us in conclusion summarize the ecological outlook of our species. The cardinal fact in the problem of the human future is the increase in the speed of change. The colonization of new countries, the change from forest to fields, the reclamation of land from sea, the making of lakes, the introduction of new animals and plants—all these in pre-human evolution were the affairs of secular time, where a thousand years are but as yesterday; but now they are achieved in centuries or even decades. One cannot estimate such changes exactly, but we shall not be far out if we say that man is imposing on the life of the world a rate of change 10,000 times as great as any rate of change it ever knew before.

In the second place, the change is becoming deliberate. What before was achieved by slow shiftings of balance due to unconscious competition is now being forced on nature at the point of human consciousness. And man is envisaging new methods of dealing with the old problems. He is tapping new sources of chemical supply and new sources of energy. He may even succeed in dispensing with green plants as prime producers, and himself obtain the manufacture of food-stuffs direct from their elements.

In all this there is promise; but there is also danger. The disadvantages of pre-human methods of evolution are their appalling slowness, their equally appalling wastefulness, and the fact that what is achieved is simply something that will work, and not something planned to work in the best and smoothest way. It is, humanly speaking, stupid that each year three-quarters of all the young that singing birds produce must come to nothing, and perhaps ninety-nine per cent. of all the seeds that are made by flowers. It is stupid that the life-community, in its task of utilizing the resources of nature, should be hampered by unnecessary

middlemen and by creatures that short-circuit the vital circulation, but that is what the unrestricted competition of life leads to, as it leads to the sufferings of bacterial disease, and to parasite cruelty. It is stupid, again from our human standpoint, that the world had to rotate on its axis some fifty thousand million times after the reptiles began to dominate it before their brainless ascendancy was brought to an end in favour of the mammals.

Yet these disadvantages involve certain countervailing advantages. Such wastage evokes enormous reserves. The exuberance which most living things must possess to survive at all in such a wasteful world is one of their beauties; and the reserves of energy, of leisure, of reproductive capacity which life must possess against the time of struggle, have been the soil out of which precious and unexpected advances have blossomed. If progress has been slow, it has been steady; if competition seems to have generated an unnecessary variety, yet it has ensured that when one type perished, new types were always present to take its place; if the communities of life are slow growths, they are adjusted and balanced growths; and epidemic disease and parasites, however cruel and wasteful, are among the checks and counterchecks by which this adjustment is maintained.

And conversely, the advantages opened up to man by the possibility of conscious quick attack upon his problems have their dangers. He can colonize a new country in record time and bring in his own appurtenances in the way of domestic animals and crop-plants; but, as we have seen, he almost inevitably upsets the balance of nature in the process and introduces devastating pests. He can make the soil produce a life-community which, like a wheat-crop, or a combination of grass and cattle, shall be most efficiently adapted to the one particular purpose he has in view; but he will be upsetting the chemical balance by removing the crop from where it grew without replacing its mineral constituents. He can tap new sources of food and energy; but too often lives on capital without putting by anything

for the future. He can eliminate economic waste; but he runs the risk of creating a life without exuberance, with all the reserves of vitality thrown into the daily struggle. He can reduce disease and the wastage of human life; he is brought up against the danger of perpetuating weakly stocks that might better never exist at all. In a word, man can see what he wants; and because he sees what he wants he can make an immediate bid for it, and change the face of things with unbiological rapidity. But he will be very unlikely by the light of nature to see all the multifarious consequences of his bid; and too often the consequences will be quite different from what he wanted, and will turn to his harm instead of his help.

What makes it possible for man to go fast is his conscious mind and deliberate purpose. But it is not enough that merely his aim and his main effort towards it should be conscious; the whole process must be conscious. He cannot leave details to Nature and expect her to be on his side. He cannot mix the new process and the old. That is why the formidable apparatus of organized research and applied science is necessary if civilization is to continue; for it is the only possible substitute for nature's clumsy sequences of secular struggle, the sacrifice of the many for the few, broadcast waste to ensure the rare lucky survival, ruthless pruning, adaptation through strife and death.

From the standpoint of biological economics, of which human economics is but a part, man's general problem is this—to make the vital circulation of matter and energy as swift, efficient, and wasteless as it can be made; and, since we are first and foremost a continuing race, to see that we are not achieving an immediate efficiency at the expense of later generations.

To this end, man, with the aid of scientific breeding and selection, can produce organisms which are quicker and more efficient transformers of matter than anything found in nature; but he can only do so if he helps nature to satisfy their increased demands. A mere truism? Not by any

means. It is true that since before recorded history cultivators and stock-raisers have used natural manure and extra fodder; it is true that in the last century, since the work of Liebig, Lawes and Gilbert, the employment of chemical manures has become almost universal. But up till quite recently man has taken little thought for the morrow beyond the single crop. It is true again that he has been forced by the demands of his wheat and corn to let his land lie fallow from time to time, or to introduce nitrogen-catching crops, like clover or lupins, into his rotation; but that is only a beginning, and the depletion of grassland we have just been considering is a reminder of the seriousness of the problem in other fields.

At last his difficulties are driving him back to first principles. In the last couple of centuries he has accelerated the circulation of matter—from raw materials to food and tools and luxuries and back to raw matter again to an unprecedented speed. But he has done it by drawing on reserves of capital. He is using up the bottled sunshine of coal thousands of times more quickly than nature succeeds in storing it; and a similar rate of wastage holds for oil and natural gas. By reckless cutting without reafforestation, he has not only been incurring a timber lack which future generations will have to face, but he has been robbing great stretches of the world of their soil and even of the climate which plant evolution had given them. This stripping the land of trees, soil, and moisture has gone on both in East and West. It is serious on the Mediterranean mountains; but it has reached its climax in China. That land is so densely populated that trees have given place to food-plants; there are often no trees at all, or only in gardens, over great tracts of country. Wood for fuel is in such parts almost unknown; the people burn straw and dung and refuse.

By over-killing, man has exterminated magnificent creatures like the bison, as wild species. Less than a century ago, herds numbered by the hundred thousand covered the

Great Plains. Buffalo Bill killed 4,280 bison with his own rifle in a year and a half; and that was far from being a record. The United States Government detailed troops to help in the slaughter, in order to force the Indians, by depriving them of their normal subsistence, to settle down to agricultural life on reservations. To-day there remain a few small protected herds.

By over-killing he has almost wiped out whales in the northern hemisphere, and unless some international agreement is soon arrived at, the improvement of engines of destruction is likely to do the same for the antarctic seas. If he is not careful, the fur-bearers will go the same road; and the big game of the world is doomed to go, and to go speedily, unless we take measures to stop its extinction. By taking crop after crop of wheat and corn out of the land in quick succession, he exhausted the riches of the virgin soils of the American west; and is now doing the same for the grasslands of the world by taking crop after crop of sheep and cattle off them. To make good these losses of the soil, he has crushed up the nitre of Chile, the guano of Peru, the stores of phosphate rock in various parts of the earth's crust. But these too are capital and the end of them is in sight. The recklessness of the nineteenth century was appalling. Linnæus gave man the title of *Homo sapiens*, Man the Wise. One is sometimes tempted to agree with Professor Richet, who thinks that a more suitable designation would have been *Homo stultus*, Man the Fool.

Man's chief need to-day is to look ahead. He must plan his food and energy circulation as carefully as a board of directors plans a business. He must do it as one community, on a world-wide basis; and as a species, on a continuing basis. In the first place, he must learn to adjust population to supplies, and not be always and only thinking of the adjustment of supplies to population. Population may soon need to be controlled as urgently as war or unrestricted individualism needs to be controlled now. In

the matter of supplies he must make provision for the future; the species must have its reserves of nitrogen and phosphorus, of timber-growth and soil-fertility, of useful animals and of sources of energy, just as surely as the Bank of England must have its reserves of gold and credit, or a factory must allow for the depreciation of its plant.

As a matter of fact, the situation is not so bad as it looks at first sight. We are using up our coal and oil; but water-power is always with us, and there are tide-power and sun-power and wind-power for us to tap. We are using up our oil; but sooner or later we shall replace it satisfactorily by power-alcohol made from plants. All over the world scientific forestry is beginning to replace irresponsible lumbering. The Peruvian Government's regulations for their guano islands have ensured that each year the birds shall contribute to the needs of the future as much as man removes for the needs of the present. The nitre-beds will be finished up, but humanity need no longer worry now that a way has been found for bringing nitrogen from the air's inexhaustible reservoirs into a form available for plants. International agreements have not only saved the Alaskan fur-seals from imminent destruction, but restored them to abundance.

In the 'seventies of last century, the herd of fur-seals on the Pribiloff Islands off Alaska numbered about two and a half million individuals. So long as animals were only killed on the islands, the number taken each year could be regulated. But private enterprise began to kill them on the high seas—with the result that by 1896 there were less than 600,000 left, and in 1911, only just over 200,000. In that year, however, all killing of fur-seals at sea was prohibited by international agreement, and by 1924 the herd numbered 700,000, and is still continuing to increase. If the whalers and the trappers and the big-game hunters are not too stupid to take similar precautions, whales and fur-bearing creatures and big game can be saved too.

In these fields man has only got to take a little trouble

and he need not fear the future. But in the matter of phosphorus, the prospects are not so bright. Phosphorus is an essential constituent of all living creatures. It is, however, a rather rare element in nature, constituting only about $\frac{1}{700}$ part of the earth's crust. In the ocean, the proportion is infinitesimal, only 5 parts of phosphate to 100,000 of sea-water. This is because phosphorus is the limiting factor for marine life. To exist at all, living matter in the sea must contain, per unit of weight, almost 100 times as much phosphorus as the surrounding water. Most of the sea's phosphorus is imprisoned in living bodies. Of all the phosphorus in the sea and in its animals and plants, some gets back to land in guano, some in phosphate deposits made of fossil bones and shells, some in fish that man catches and brings ashore; but all this is a trifling fraction of the whole, and for the most part slow-accumulating. On land, meanwhile, the soil is losing phosphorus all the time, partly by leaching out into rivers, partly by crop depletion. From the soil of the United States alone the equivalent of some six million tons of phosphate is disappearing every year; and only about a quarter of this is put back in fertilizers. Meanwhile, the store of fertilizers is being depleted, and man (*Homo stultus* again !) is sluicing phosphorus recklessly into the ocean in sewage. Each year, the equivalent of over a million tons of phosphate rock is thus dumped out to sea, most of it for all practical purposes irrecoverable. The Chinese may be less sanitary in their methods of sewage disposal, but they are certainly more sensible; in China, what has been taken out of the soil is put back into the soil. It is urgently necessary that Western "civilized" man shall alter his methods of sewage disposal. If he does not, there will be a phosphorus shortage, and therefore a food shortage, in a few generations. But even if he does that he will still have to keep his eye on phosphorus; it is the weak link in the vital chain on which his civilization is supported.

INDEX

(Page numbers in black type indicate illustrations)

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